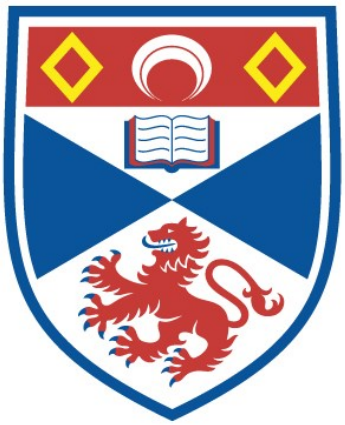
VISUAL RESPONSES IN LOCUSTS

George K. Wallace

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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A Thesis Presented for the Degree

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by

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CERTIFICATE.

I certify that George K. Wallace, B.Sc., has spent the equivalent of nine terms at research work under me, and that he has fulfilled the conditions of Ordinance 16 (St. Andrews) so that he is qualified to submit the accompanying thesis in application for the degree of Ph.D.

Natural History Department,
Queen's College,
DUNDEE.
January, 1958.

DECLARATION.

I hereby declare that the following thesis is a record of results obtained by me in the course of research on Visual Responses in Locusts and further that the thesis is my own composition and has not previously been presented for a higher degree.

UNIVERSITY AND RESEARCH TRAINING.

I commenced my University studies at Queen's College (then University College) Dundee, of the University of St. Andrews in 1950. In 1953 I took a B.Sc. degree in Botany and Zoology and in 1954 I was awarded First Class Honours in Zoology for research on the anatomy of the Sawfly compound eye.

I was then awarded a Carnegie Scholarship and a Cross Trust Scholarship to allow me to pursue research for the degree of Ph.D. (St. Andrew's). This research was carried out in the Hope Dept. of Entomology, Oxford, during the period 1954 - 1957.

I now hold a Nuffield Senior Research Scholarship in the Dept. of Psychology, Reading University.

VISUAL RESPONSES IN LOCUSTS.

CONTENTS.

Page.

ACKNOWLEDGEMENTS

INTRODUCTION 1

MATERIAL 8

FORM PERCEPTION

Introduction 10

Experiments 12

The Importance of Regions of Contrast 13
Experiments with black objects on a white background 15
Different sized stripes 16

The Importance of Contrast 16

The Importance of Area and Height 19

The Importance of the Vertical Edge 25

The Importance of Position 26

The Importance of a Vertical straight edge as opposed to an oblique straight edge. 28

The Importance of a straight vertical edge 29

The possibility of an I.R.M. for a straight vertical edge 31

The Importance of Articulation 33

Discussion 34

PEERING

Introduction 45

Method of Measuring Peering Angles 46

Peering - a Visual Response 47

Peering and Orientation 51

Page

PEERING CONT'D

Peering and Distance Estimation 54

Peering - A General Discussion 66

ANTENNA WAVING

Introduction 70

Experiments 71

Flicking 73
Flicking - Discussion 75

Beating 76
Antenna Beating - Discussion 86

The Biological Significance of Antennal Movements as Released by visual stimuli 89

Antennal movements and distance estimation 92

RESPONSE TO MOVEMENT

Introduction 93

Fright Response to a moving object 94

Optomotor Responses 97
Stimulus 97
The Effect of a small part of the visual field 98
Stimulation of different parts of the eye 100
Importance of the Type of Movement 100
Discussion 101

Subject and Object Movement 102
The von Buddenbrock Experiment 103

The differentiation of Subject and Object movement 107
Principle 108
Experimental conditions 109
Control 112
Discussion 113

Response to Movement - Discussion 115

Page.

GENERAL DISCUSSION 116

Total number of ommatidia stimulated and speed of image movement 119

Attractiveness of objects 120

Speed of image movement and position on the eye 121

Subject and Object Movement 122

Possible elaboration of an integrating system dealing with visual stimuli 125

CONCLUSION 128

SUMMARY 129

APPENDIX 135

REFERENCES

TABLES (fold out at back)

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Dr. Uvarov and Dr. T. H. C. Taylor of the Anti-Locust Research Centre gave me much encouragement in this research. Through them I was also given access to much of the locust literature and in addition awarded a grant for apparatus.

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Finally I wish to thank my wife for her helpful criticism and encouragement.

INTRODUCTION.

In many insects the compound eyes are extremely prominent. They are a pair of rounded protuberences, the surfaces of which, under closer examination are seen to be divided into numerous hexagonal facts. Each of these facts is the outer extremity of a visual receptor unit - an ommatidium.

Naturally such conspicuous structures have attracted much attention and Zoologists have been studying the functioning of these organs for many years. Ever since Exner's classic treatise "Die Physiologie der facettirten Augen von Krebsen und Insekten" was published in 1891 there has been an almost continuous output of information on the subject. Nevertheless, although to-day the literature is legion, large lacunae still remain.

Three main approaches are usually made, the anatomical, the physiological and the behavioural. The anatomical work consists in cutting sections of the head and eyes and studying the detailed structure of the ommatidia and their arrangement. The literature on this aspect of the subject is too numerous to mention in full but the work of Nowikoff (1931) and del Portillo (1936) are good examples. Very detailed studies have also been made of the anatomy of the optic ganglia (Cajal and Sanchez 1915; Zawarzin 1914 in Roeder 1953).

In the physiological field, nerve impulses have been recorded from the optic ganglia, optic nerve and whole retina in response to different

stimuli. This work has been recently reviewed very comprehensively by Wulff (1956).

The behaviour studies consist of observing the behaviour of the intact animal usually in response to controlled experimental conditions of visual stimulation. In this field the work of Hertz, von Frisch and Buddenbrock are well known (see bibliography for individual references). There are many other workers who will be referred to in the body of the text where their work is described in more detail.

Two or more of the above aspects are frequently combined, e.g. Baumgärtner (1928), Bauers (1953) and a behaviour reflex may be studied in order to obtain physiological measurements, e.g. Hecht and Wolf (1927) measuring visual acuity and Schneider (1956) measuring spectral sensitivity. In fact it is becoming increasingly clear that, only with a knowledge of all the aspects mentioned, can it be hoped to ask meaningful questions with regard to the working of the compound eye. Consequently the results of the anatomist and physiologist are basic to any behaviour study such as the present one.

In the past the behaviour approach has elicited much useful information. From it it is known that some insects tend to go towards light some away from light (Fraenkel and Gunn 1940). In other cases such as bees and butterflies, not only can the insects perceive differences in light intensity but they can detect differences between certain forms and patterns (Hertz, see bibliography; Ilse, 1932). Some insects can

perceive certain colours in some cases the sensitivity extending into the ultra-violet region of the spectrum. Colour vision in insects is reviewed by von Buddenbrock (1952)(see also Wulff 1956). Responses to polarised light have been demonstrated in bees (von Frisch 1949, 1950) in ants (Vowles 1950, 1954a, 1954b) and a sawfly (Wellington 1953). Many varied responses have been obtained to movements in the environment (see references in text p. 93) and some insects have been shown to estimate short distances very accurately by a binocular method basically the same as that in Man (Baldus, 1926; Friederichs, 1931). In short, such behaviour studies have provided some idea of the visual world of the insects in question. This is the aim of the present investigation.

In this present work the term "visual response" is defined as any piece of behaviour pattern released or guided by visual stimuli. This thesis is an account of the study of a few such responses in the nymphs of the Desert Locust, (Schistocerca gregaria (Forskål).[1]

Very little is known of the part played by vision in the behaviour of locusts in general and Schistocerca in particular. It is believed (Kennedy, 1939) that, in conditions of moderate or low light intensity (below 1,000 metre candles) and when not too active, nymphs and adults of Schistocerca exhibit positive phototaxis,[2] i.e. they move towards a

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1. The insect was originally described under Gryllus gregarius by Forskål in 1775. The name Schistocerca gregaria was fixed by Uvarov in 1923 and the common name Desert Locust was coined by that author in 1928. Hereafter for convenience it is referred to as Schistocerca or the Desert Locust.
2. These conditions are fulfilled in the laboratory experiments reported in this thesis. The light intensities were well below 1,000 metre candles and very active insects were never used.

light source (Fraenkel and Gunn 1940). Volkonsky (1939) showed that Schistocerca performs a non-locomotory orientation to a light beam and that this orientation is accomplished partly with the aid of visual stimuli, a movement of the light source eliciting a compensatory movement of the body. Again, the nymphs of Schistocerca are attracted to one another (Ellis 1956) and it is possible that vision plays a large part in this as it appears to do in the case of the migratory locust Locusta migratoria migratorioides (Ellis 1953 and personal communication).

As can be seen from the above the information available is very fragmentary and at best gives little idea of the visual world of this insect. There is no doubt however that vision plays an important part in the behaviour of this insect as has been strongly indicated by field observations (in particular Kennedy, 1939; 1945).

As a subject for the study of behaviour in relation to visual stimuli Schistocerca is ideal. Since it is an exopterygote, as are the other Orthoptera, there is only slight metamorphosis from nymph to adult. There are five nymphal stages plus the adult stage. In the fifth nymphal stage, which is the one mainly used in this present work, the compound eyes are well developed and possess about 7,685 facets (i.e. this number of visual receptors)(Bernard 1937). Roonwal (1947) showed that the eyes were of an anatomical type (apposition type) which is thought to be particularly efficient for the perception of forms and movements (Wigglesworth 1953). The visual field is large - 225° in the horizontal plane - and the fields of both eyes overlap in front giving a 60° arc of binocular

vision anteriorly (these measurements are for the 5th instar nymphs, Whittington, 1951 unpublished).

Apart from the advantages of the well developed eyes the insect is large, robust and easy to handle (length increases from 0.33 mm. to 0.45 mm from the beginning to the end of the 5th instar. Uvarov 1928). This large size of the body and appendages makes it relatively easy to observe small details of behaviour and contributing to this is the fact that, when undisturbed, the nymph moves fairly slowly. Finally, the flightlessness in the nymphal stages makes the construction of suitable experimental apparatus much easier than in the case of a flying insect.

The thesis is divided into four experimental sections as follows:-

I. Form Perception.

II. Peering.

III. Antenna Waving.

IV. Responses to movement.

The form perception section stemmed directly from the results of previous workers. Even if there were no great development of form discrimination in Schistocerca to the extent that there is in bees, nevertheless some response to objects was extremely likely. The support for this comes from the work of Hundertmark (1937b) who showed that even lepidopteran caterpillars with only groups of ocelli have some degree of form discrimination. Sawfly caterpillars possessing two large ocelli show an attraction to vertical black/white edges (Wallace 1954 unpublished). It did not seem unreasonable, therefore, to expect that some response to

form would be present in Schistocerca where the compound eyes are so well developed.

The "peering" and "antenna waving" sections stemmed from the form perception section in that both peering and antenna waving were pieces of behaviour observed during the orientation and attraction to forms. Both responses were shown to be visual responses and were studied in detail.

Throughout the work there was an increasing suggestion of the importance of movement as a stimulus and this culminated in a brief general survey of this in the last section. It was in fact shown that all the responses observed could probably be explained on the basis of a response to movement. The effects of different sorts of movement were studied.

A behaviour approach of this kind is fraught with one major initial difficulty. This is that the perceptual world of the insect studied is probably very different from that of the observer. Now, in the behaviour of Man, vision plays such an important role that it is difficult to approach any objective study of insect vision without at least a few preconceived ideas. To guard against this the a priori assumptions (and a few are inevitable) must be kept to a minimum. In this thesis this has been done with great stringency. For example, it is first shown that the insects are attracted to regions of contrast before any study is made of responses to complex forms. Again, the objects and patterns used throughout this work have been two-dimensional. Almost nothing is known about the part played by three-dimensionality in the visual environment of insects. Much of the perception of this property depends, in the

case of human vision, on knowledge of perspective, on interpretation of shading and on differences of focus. Since there is, as yet, no evidence of the operation of these mechanisms in insects the perception of three-dimensionality in this case cannot be assumed. Finally, black and grey objects have been used against white backgrounds for there is no good evidence at present to show that the insect can perceive colour.

The thesis thus resolves itself into the question of what the insect can do with a limited number of simple visual stimuli, the use to which visual information is put and the methods of obtaining this. Often the result is surprising and the responses apparently quite complex. Implicit in this approach is the concept of the compound eye as a navigating instrument for, in the last analyses, the function of the sense organs is to enable the animal to move about freely in its environment.

The results give some idea of the visual environment of Schistocerca gregaria although time has not permitted the study of colour or polarised light, two stimuli which may well form an important part of this environment. As will be pointed out, certain details of this visual environment which is that of a crawling insect (in the nymphal stages used) may differ importantly from the environment of a flying insect. It is probable, however, that many of the principles investigated here apply to all insects with well developed compound eyes and some may extend over even a wider field involving other animals.

MATERIAL.

Schistocerca gregaria is a polymorphic species existing in a range of forms which differ morphologically and biologically. The extremes of this range have been called phases. In one phase the insect is a solitary grasshopper, this is the phase solitaria. In the other it is a typical swarming locust, this is the phase gregaria. (Uvarov 1928). By definition a locust is a grasshopper with a swarming phase (Uvarov 1928). In the phase gregaria the nymphs are dark in colour, in the later instars the general coloration is yellow or orange-yellow with a strongly pronounced black pattern (after Uvarov 1928). The eyes are darkly pigmented. Nymphs of the phase solitaria are pale green in colour with sometimes traces of black markings. The eyes are pale with vertical stripes. For a description of the eyes of the two phases see Roonwal 1947. In the present investigation only nymphs of the phase gregaria were used.

The insects were obtained from the Anti-Locust Research Centre, London, usually either as first instar nymphs or as eggs laid by gregaria adults. (In a few cases 4th or 5th instar nymphs were obtained). The nymphs were reared in crowded conditions, about 600 first instar nymphs to a cage 18 inches square by 12 inches high. By the 5th instar there were approximately 300 insects per cage.

Two opposite walls of the cages were of wire gauze to allow air to circulate freely. The other walls were of hard-board and the top was of glass. The cages were kept overnight in a constant temperature room maintained at 28° C. During the day, the cages had to be moved outside

the constant temperature room since space was limited and other experiments were in progress. However, by means of electric light bulbs suspended above the cages the temperature was maintained at a reasonably high level (26 - 32°C).

The insects were fed each evening with fresh grass standing in water.

Under the conditions described the insects developed the typical gregaria coloration.*

Care was taken to ensure, as far as possible, that the nymphs were not over active or highly excited when they were used for experiments. This was achieved by judicious feeding. It was found that if nymphs were tested in the morning (10 a.m. to about 12 noon) they did not require any feeding other than the routine feeding the previous evening. Nymphs tested later than this were fed two hours before testing. Despite these precautions variations in excitability were still encountered probably due partly to the response of different individuals to handling or to differences in physiology of the individuals.

The experiments were performed in the constant temperature room at 28°C. Whenever possible the only light present was the one used to illuminate the apparatus. At times when, unavoidably, other experiments were in progress any apparatus described here was screened off from the influence of extraneous light. There was no indication that such external light interfered with the responses of the insects.

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* Except that the development of the yellow colour is slightly belated in laboratory stocks.

FORM PERCEPTION.

Introduction.

One of the main features of the visual field is the presence of objects. In several cases it has been shown that insects respond to objects in the environment, and that the responses are mediated partly by vision of the form of these objects, e.g. bees and butterflies are attracted to flowers (von Frisch 1914; Ilse 1932), and stick insects are attracted to black stripes representing stems (Kalmus 1937).

In the simplest analysis, objects appear merely as areas of the visual field, the reflected light from which differs quantitatively and/or qualitatively from the light reflected from their surroundings. The presence of objects in a visual field can thus be detected by a simple photo-receptor sensitive enough to record small changes in light intensity, but the perception of the form of such objects requires a more complex receptor. Indeed, Buddenbrock (1935) sees form perception ability as the sharpest distinction between higher and lower compound eyes.* Thus he states that, in some beetles and other insects with even less well-developed eyes, no reaction to form could be obtained, nor was there any other evidence of form perception in these animals. To show that an animal can perceive form it is not sufficient to show that it can see objects, it must be shown that the animal can distinguish one from another.

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* It must be remembered, however, that an ability to discriminate between simple forms exists in some caterpillars (Hundertmark 1937b).

Amongst insects this ability to discriminate between forms has, however, been clearly demonstrated in bees (von Frisch 1914; Baumgärtner 1928; Hertz 1929a, 1929b, 1931, 1933, 1934c, 1935, 1937), and in butterflies (Ilse 1932). The ability of the wasp Philanthus to distinguish between arrangements of small objects (van Beusekom 1948) is also evidence of form discrimination.

Of form perception in Orthoptera little is known. Kalmus (1937) showed that stick insects (Dixippus morosus) were attracted to vertical black/white boundaries and to black stripes on a white background (see also Hundertmerk 1937c). Williams (1954) worked with the grasshoppers Chortippus parallellus (Zetterstedt) and Comphocerippus rufus (L.) and concluded that they possessed the ability to discriminate between forms, but his evidence is not detailed and gives little indication as to which properties of the figures are involved.

It is generally accepted that the efficiency of a compound eye for forming the image of figures is measured to a great extent by the number of the facets. Thus, ..."the retinal image....consists of a mosaic of points of light.....a mosaic which will be coarse or fine depending on the number of facets per unit area". (Wigglesworth 1953). The "apposition"* type of compound eye is thought to give a sharper image than the superposition type of eye. The former is the type of eye found in the nymphs and adults of Schistocerca gregaria (Roonwal, 1947) and it has numerous facets (e.g. 4th instar nymph 6,480; 5th instar nymph 7,685 (Bernard 1937)). Thus according to current belief both nymph and adult

* See notes on this in appendix.

possess the requisite apparatus for form discrimination (at least at the level of the retina). The aim of the present work, therefore, was to investigate form perception ability in the nymphal stages of Schistocerca and to compare the results with those which had previously been found for bees where the basis of form perception had been studied in greatest detail (Hertz 1929, etc., Wolf and Zerrahn-Wolf 1936). It was also considered a matter of interest whether or not the basis of form perception and the attractive properties of forms were the same for a walking insect (locust nymph) as for a flying insect (bee).

The problem was thus to find, firstly, if locust nymphs were attracted to objects in the environment* and secondly, if the insects could distinguish between the forms of these objects.

Experiments.

Apparatus and Procedure.

The basic method used in all the form perception experiments was to place an animal in the centre of a large circular arena (diameter 2 ft.) whose vertical 10" walls were decorated with the patterns to be tested. The subsequent behaviour of the animal was observed. In this way the animals were allowed to choose spontaneously between the forms presented.

Lighting was from an overhead source so arranged as to give equal illumination over all parts of the arena with no heating effect. All

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* The first part of this work was completed before the appearance of Chapman's paper (1955) which provided evidence on this point.

experiments were performed in a constant temperature room at 28°C. The animals were fed before testing so as to reduce their activity. Further details of the nymphs used in each particular test, i.e. instar and number of times tested, are given under the separate experiments.

The Importance of Regions of Contrast.

Experiment 1: Preliminary experiment. Equal areas of black and white.

Schistocerca gregaria is known to be photopositive (Fraenkel, 1929, Kennedy 1945), as are many other ~~cercadidae~~ Acrididae (See Grassé 1923, Chapman 1954, 1955). It was thus possible that, if the nymphs were placed in a heterogeneous environment consisting of equal areas of black and white, they might show an attraction to the white patches. On the other hand Ellis (1953) showed that in the case of Locust migratoria, when not sitting with other nymphs, the insects preferred to sit near black objects rather than white ones. This was on an almost white background. It was possible therefore that in this case the Schistocerca nymphs might be found to choose the black areas of the environment. Again, it was possible that they would be attracted to black/white boundaries, c.f. stick insects (Kalmus 1937). The present experiment was designed to test these possibilities.

Forms. The circumference of the arena was 72" and this length of wall was divided into eight equal sections, four black and four white. Each section thus measured 9" broad by 10" high and a black alternated with a white. Thus, to an animal in the centre of the arena, the immediate visual field consisted of four white areas and four black areas.

The animals had, therefore, an equal chance of approaching a black or a white area. The floor was of plain white paper.

Animals. These were 5th instar nymphs of the normal gregaria phase.

Behaviour. An animal placed in the centre of the arena remained stationary for a short period (usually $\frac{1}{4} - \frac{1}{2}$ minute). It then swayed the front part of the body slowly from side to side several times before starting to walk. This swaying of the boyd is called "ppering" (Kennedy 1945), and is more fully described later (p.45). The animals were found to approach the wall of the arena, in some cases stopping from time to time, peering and occasionally changing direction.

The above describes the typical behaviour seen in all the form perception experiments.

Readings. When the insects had reached the wall, the point at which they first touched it was noted. The readings were divided into three categories, (1) animals going to the black areas; (2) those going to white areas; (3) those going to the vertical black/white boundaries between the areas.

The experiment was repeated several times. 30 runs were performed with 30 different animals.

Results. The results are given in table 1. They show clearly that the majority of the insects were attracted to the vertical black/white boundaries, ($p < .01$)(see notes on statistics with tables at back). Very few

insects were attracted either to the black or the white, equal numbers going to each.

Conclusion. It was concluded that locust nymphs are attracted to vertical black/white boundaries.

Experiments with black objects on a white background.

The first experiment had shown that the insects were attracted to the regions of contrast in the visual field. They had, however, been presented with equal areas of black and white, a situation rather far removed from the normal. The natural visual environment consists of relatively small objects seen against a relatively larger background. It was therefore decided to decrease the size of the black areas and increase the size of the white so as to present the animals with several black objects on a large white background.

From now on, all the form perception experiments described, followed exactly the same procedure. The background was supplied by the white wall of the arena on to which the objects were fixed so as to touch the floor. The objects were cut out of thin card, painted black with indian ink and fastened to the wall with concealed strips of sellotape.

The method of measuring the relative attractiveness of the forms was to present the animals with eight objects, four of one shape and four of another and to count the number of animals going to each. The objects were placed at equal intervals and an object of the one shape alternated with an object of the other. After each few runs the cylinder

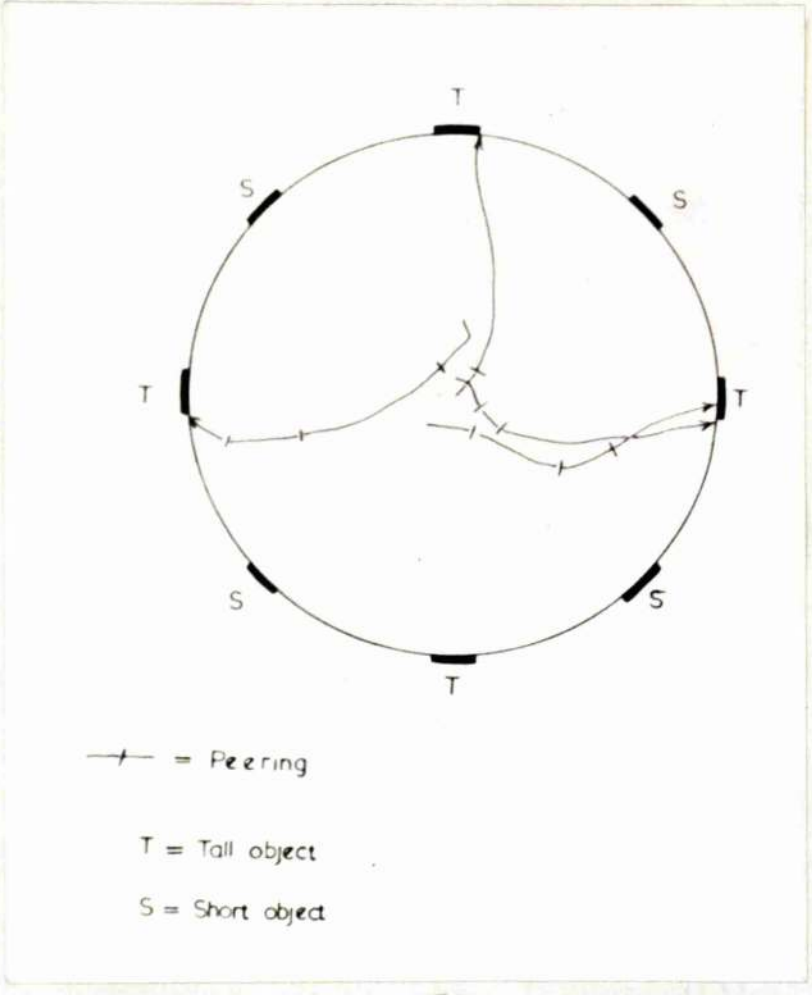

Fig. 1.

Diagram showing specimens of the tracks made by locust nymphs in a white walled arena with black vertical stripes on the wall.

was rotated with respect to the paper floor and at intervals the paper floor was renewed. In this way the possibility of the animals following scent trails of any description was removed.

Experiment 2: Different sized stripes.

Forms. Four tall black stripes 10" high X 2" broad and four short black stripes 5" high X 2" broad.

Animals. 5th instar nymphs of the normal gregaria phase. 40 runs were made with 40 different animals.

Results. The numbers going to the tall and short stripes were noted, as well as the numbers going to the vertical edges of the stripes. An animal was counted as going to an edge if it hit the wall within .5" of an edge. The results are presented in table 2.

The results show that the insects were attracted to the black figures, showing a highly significant preference for the taller figures ($p < .01$). Furthermore, the insects were clearly attracted to the vertical edges of the stripes. Fig. 1 shows a specimen of the tracks recorded.

Conclusions. It was concluded that locust nymphs are attracted to tall black rectangles on a white background. The taller the rectangle the more attractive it is.

The Importance of Contrast.

Experiment 3. Black stripes and grey stripes.

The aim of this experiment was to test further the importance of the contrast between the object and the background. The animals were

given the choice of black stripes and grey stripes of the same size.

3a. Forms. Black stripes 10" tall X 2" broad. Grey stripes (N 5.5 of the Munsell series) 10" tall X 2" broad. This grey is fairly dark.

Animals. 4th instar* phase gregaria. 10 animals tested each 5 times.

Results. The results are given in table 3 and show that the grey used in this experiment was as attractive as the black ($.5 > p > .3$).

3b. In this experiment a lighter grey was used.

Forms. Four black stripes 10" tall X 2" broad. Four grey stripes (YR 10 7/1 of the Munsell series) 10" tall X 2" broad.

Animals. 5th instar, phase gregaria. 10 animals each tested 5 times.

The experiment was repeated with 4th instar nymphs. 20 were tested each 5 times.

Control. In the control experiment the insects were presented with 8 light grey stripes.

Results. The results are given in table 4. In contrast to the results obtained in experiment 3a, the results now obtained showed that there was a highly significant preference for the black stripes ($p < .01$ in each case). It was not the case that the grey stripes were not visible

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* There did not appear to be any important difference between the behaviour of the 4th and 5th stage nymphs. Further observation confirmed this. Usually, however, 4th stage nymphs were never used except when 5th's were not available.

UNIVERSITY OF ST. ANDREWS

DJ/JLM.

COLLEGE GATE,
ST. ANDREWS.

From
The Dean of the Faculty of Science,
David Jack, M.A., Ph.D., F.R.S.E.

5th March, 1958.

Dr. J.M. Dodd,
Department of Natural History,
ST.SALVATOR'S COLLEGE.

Dear Dr. Dodd,

The following Committee has been appointed to examine the Ph.D. Thesis submitted by Mr. G.K. Wallace:-

Dr. Waterhouse (Convener),
Professor Callan,
Dr. Dodd.

As Dr. Waterhouse has already seen the Thesis, I should be obliged if you would return the enclosed copy to Mr. Ritchie after you have seen it.

Yours sincerely,

Jack.

Dean.

to the insects for the controls showed that, in the absence of the black stripes, the animals orientated perfectly well to the light grey ones.

Conclusion. Experiment 3 demonstrated that, on a white background, the darkness (blackness) of an object is an important property affecting the attractiveness of the object. However, at this point a cautionary word must be inserted. It is known from the work of Hertz (1937) that surfaces, which to our eyes appear grey, appear to bees as definite colours. If the same is true of locusts then it is possible that the greys used in the present experiments appeared to the insects as distinct colours. On the other hand, the first grey which was used was equally as attractive as the black and it was a dark grey which suggested that the insects were indeed responding to the contrast between object and background. Furthermore, observation clearly showed that the insects were orientating to the vertical edges of the objects, i.e. the regions of contrast, in the case of both the black and grey stripes.

Whether or not locust nymphs see greys as colours cannot be decided without a further series of detailed experiments. Although no readings were taken of it in this experiment, observation showed that the animals were again orientating to the vertical edges of the stripes rather than to their centres. The findings thus suggested that the black objects were attractive because, when seen on the white background, they had a sharp vertical edge.

The Importance of Area and Height.

The results of the experiment with tall and short stripes (expt. 2) had now to be reconsidered. In the light of the obvious importance of the vertical edge it was tempting to suppose that the greater attractiveness of the tall stripes was due to their possessing longer vertical edges. However, although it had been shown that, when approaching a stripe, the insects orientated towards the vertical edge, there was no evidence to show that the edge of the stripe was what had initially attracted the insects. The taller stripes differed from the shorter ones in two ways, first, they had a larger area (20 sq." as against 10 sq.") and secondly they had longer vertical edges. Both stripes were black and therefore the sharpness of their edges was the same. Their breadths were equal. Thus, either the greater area of the tall stripes, or their longer vertical edges could be the cause of their greater attractiveness.

It was therefore decided to test separately the importance of the two properties area and height. This was to be done by presenting the insects first with stripes of constant height but different area and second with stripes of constant area and different height.

Experiment 4. Stripes of equal height and different area.

4.a. Forms. Black stripes 10" tall X 2" broad. Black stripes 10" tall X 4" broad. In the table of results the former stripes are called "narrow" and the latter "broad". The area of the broad stripes was, of course,

twice that of the narrow.

Animals. 5th instar, phase gregaria. 10 animals tested each 10 times. The experiment was repeated with 4th instar nymphs of the phase gregaria. 10 animals were tested each 5 times.

Results. The results are given in tables 5a and 5b. They are extremely surprising, for, contrary to showing either a choice of the larger objects or an equal choice of both, the animals showed a highly significant preference for the narrower objects ($p < .01$ in each case).

Conclusion. It was clear from the results that the objects of smaller area were certainly the most attractive. The question now was, what made the narrower stripes so attractive by comparison? In both experiments the tracks of the animals had been recorded on pilot sheets and it was quite clear that here again the animals were orientating to the vertical edges of the stripes. The only difference between the vertical edges of the narrow stripe and those of the broad stripe was that in the former the two edges were closer together while in the latter they were further apart. It was thus possible that herein lay the explanation of the greater attractiveness of the narrower stripe. The argument could be put as follows:-

It has been suggested that when an animal orientates to an object it turns towards the object and brings the image of it on to a fixation region of the eye - the region of the forwardly directed ommatidia. If, due to any deviation in the insect's track, the image moves this front part of the eye, the insect corrects, i.e. re-orientates to bring

the image once more on to the fixation region. (Fraenkel and Gunn 1940). It was possible that the animals preferred to orientate to the narrow stripe because it allowed both vertical edges to be "fixed" by the anterior part of the eye, whereas in a broad stripe the vertical edges were too widely separated to be so "fixed".*

4.b. Subdivision of the broad stripes.

If, as suggested above, the insects were choosing the object whose vertical edges were closer together and not just the object of smaller area, it should be possible to increase the attractiveness of the broad stripes by adding a vertical black/white edge between the two outside edges. The present experiment was to test this.

Forms. These were the same as the forms used in the previous experiment, except that each broad stripe was subdivided by a very narrow white stripe (.25" broad) running vertically down the centre. i.e. black stripes 10" tall X 2" broad; black stripes 10" tall X 4" broad + narrow central white stripe.

Animals. 4th instar, phase gregaria. 20 animals, each tested 5 times.

Control. The control was done by removing the narrow white stripes and thus returning to the original situation of broad and narrow stripes.

Results. These are given in tables 6a and 6b.

The controls showed that there was a preference for the narrower stripes as has been found previously. When the boad stripe was sub-

*As will be seen later, there is a simpler explanation for the attractiveness of the narrower stripes. See the discussion at the end of this section.

divided, the bias was altered and there was equal choice of the broad and narrow stripes. ($.2 > p > .1$). The difference between this and the control experiment was highly significant ($p < .01$).

Conclusions. In the situations presented to the insects in these experiments 4a and 4b, it had thus been shown that larger area did not make a figure attractive if, at the same time, the distances between the vertical edges was too great. The presence and position of these edges appeared to be more important than area. It was still possible, of course, that, in smaller figures whose breadths were not so great as to separate the vertical edges too widely, area might prove to be important. The following experiment tested this.

Experiment 5. Stripes of medium breadth and very narrow stripes.

Forms. Black stripes 5" tall X 2" broad (broad stripes). Black stripes 5" tall X .25" broad (narrow stripes).

The broad thus possessed four times the area of the narrow ones, however, the broad stripes were only 2" broad and it had already been shown that stripes of this breadth were not too broad and were attractive to the insects. (expts. 2, 3, 4).

Animals. 4th instar, phase gregaria. 20 animals, each tested 5 times.

Results. These are presented in table 7. The animals were found to show a preference for the broader stripes ($.02 > p > .01$).

Conclusions. The broader stripes, in this experiment, now proved to be more attractive than the narrow ones. Now, the argument, as put

forward above, to explain the importance of the width apart of the vertical edges could not apply in this case, for here the insects were choosing the wider stripe. It seems reasonable to suppose that, in this case, the animals made their choice in favour of the largest area. Possibly, at a distance, the broader stripe is more distinct than the narrower one, which will only subtend a very small horiztonal angle.

In su ming up, then, it can be stated that, when all stripes are of equal height, a stripe of intermediate breadth (2") is preferred either to a very broad stripe (expt. 4a) or to a very narrow stripe (expt. 5), the important factor in the first case being the distance apart of the vertical edges and in the second case the area.

The original purpose of the experiments on breadth had been to test the effect of increased area for constant height in an attempt to explain the attractiveness of a tall stripe 10" X 2" over a short stripe 5" X 2" (expt. 2, p.6). It was now seen that the effect of area was unpredictable and that area did not seem to be as important as the vertical stripe edges. The results of experiments 4a and 4b had again pointed to the importance of these edges (p.20-21). The importance of the height of this vertical edge was now studied.

Experiment 6. Stripes of equal area and different height.

Forms. Tall black stripes 6" tall X 1" broad. Area = 6 sq.". Short black stripes 3" tall X 2" broad. Area = 6 sq".

Animals. 5th instar, phase gregaria. 20 animals, each tested 5 times.

Control. A control experiment was done by removing the tall stripes and presenting the insects with the four short ones.

Results. These are given in table 8. The animals showed a very significant preference for the taller stripes. The shorter stripes were almost entirely ignored (only 9 hits) although the controls showed that, in the absence of the taller stripes, the shorter stripes were attractive to the insects. ($p < .01$).

In the experimental runs the behaviour of the insects made it clear that, in many cases, they were making their choice from the centre of the arena, turning so as to face the taller stripes. In one case a nymph was seen to face a particular tall stripe, the arena was then rotated slightly (the floor remaining stationary). After approximately 2 seconds the animal reorientated in the new direction of the tall stripe. In the controls the insects were again seen to face the stripes from the centre, showing that the short stripes were perfectly visible from the centre of the arena where the choice was made.

Conclusion. It is concluded that, under the conditions reported, the figure of larger vertical edge is the more attractive.

Experiment 7. Objects of equal area and equal perimeter.

It was just possible that, in the previous experiment, the animals chose the taller stripe because it possessed a larger perimeter than the short stripe (14" as against 10") although this was thought unlikely. Experiment 7 was designed to clarify this point.

Forms. Black rectangle 2" X 1" with longer edges vertical. Black

rectangle 2" X 1" with longer edges horizontal. Of necessity the objects were small for the largest side could not be more than 2", otherwise the breadth of the horizontal figure would complicate matters. (In later figures (expts. 11, 12, 13) the breadth was 3" but this was not important since all the figures were of the same breadth).

Animals. 20 5th instar nymphs each tested 5 times.

Results. The results are given in table 9. They show that, for objects of equal area and perimeter, the more attractive are those with the largest vertical edge. The number of misses was large, undoubtedly due to the small size of the figures, for, from the centre of the arena, the angle subtended by the objects was very small.

Importance of the vertical edge.

All the experiments performed had demonstrated, by process of elimination, the unique importance of the vertical edges of the objects used. The experiments had been instigated in an attempt to explain why tall stripes should be more attractive than short stripes, as found in the initial experiment (expt. 2). There was now no doubt that the tall stripes were more attractive, not by virtue of their larger area (since a large area is not always attractive, expt. 4, and the taller stripe is chosen even when the areas of the stripes are the same, expt 6), nor by virtue of their larger perimeter (since a difference in perimeter is not necessary, expt. 7), but by virtue of their longer vertical edges (all expts. point to the importance of the vertical edge, particularly expt.

4b p.21).

Henceforth attention was focused on the qualities of this edge. These were (a) position, (b) verticality, and (c) straightness.

The importance of position.

The term position should be further clarified. Perhaps this can best be achieved with reference first to human vision. In Man, when the body and head are in the erect posture the eyes look along a line of sight parallel to the ground, i.e. horizontal. When the person is standing on a flat horizontal surface with the eyes at first looking horizontally, any object so situated that the head or eyes have to be tilted up to look at it must be situated vertically with reference to the plane on which the observer is standing. Now, because of the structure of the compound eye, insects do not have to move their heads to see such an object, it will be seen by ommatidia more towards the top of the eye. Was it possible then, that an object whose image appeared on the upper ommatidia, was more attractive than a similar object seen by the more horizontally directed ommatidia? In other words, did an image appearing on the more upwardly directed ommatidia signify a tall object for the insects? (What might be called an IRM releasing attraction to a tall object, Tinbergen 1951). The possibility was tested in the following experiment.

Experiment 8. Objects in high and low positions.

Forms. Black rectangles 3" tall X 2" broad, bases on the floor of the arena, Black rectangles 3" tall X 2" broad, bases 3" above the floor. The tops of the objects were therefore at 3" and 6" above

the floor respectively as had been the case with the objects 6" X 1" and 3" X 2" in expt. 6 where the taller objects had been preferred).

Animals. 5th instar, phase gregaria. 10 animals each tested 5 times.

Results. The results (table 10) showed that a significantly greater number of the insects went to the lower objects ($.05 > p \geq .02$).

Conclusion. The results of this experiment are difficult to interpret. The figures show that a majority of the insects went to the lower objects. However, it was occasionally seen that insects heading for one of the higher objects turned aside when close to it and went to the low object nearby. It is not possible to say exactly how often this happened, i.e. how often the primary orientation was to the higher object, for often one cannot tell with any certainty to which object the insect is orientating until it is fairly close to it.

From the behaviour of the insect in this experiment a reasonable conclusion would seem that probably both objects were equally attractive from a distance, and that the apparent preference for the lower object was due to the insects 'losing their way' when close to the higher object and reorientating to the lower one. With reference to the original question of the attractiveness of a tall object it would therefore appear appear that this object was attractive, not because its edge stimulated more dorsally directed ommatidia but because it possessed a longer vertical edge. Whether the loss of orientation when close to the higher object is due to the object's foreshortening in that position, or to the fact that the insect can only orientate when the more forwardly directed

Fig. 2

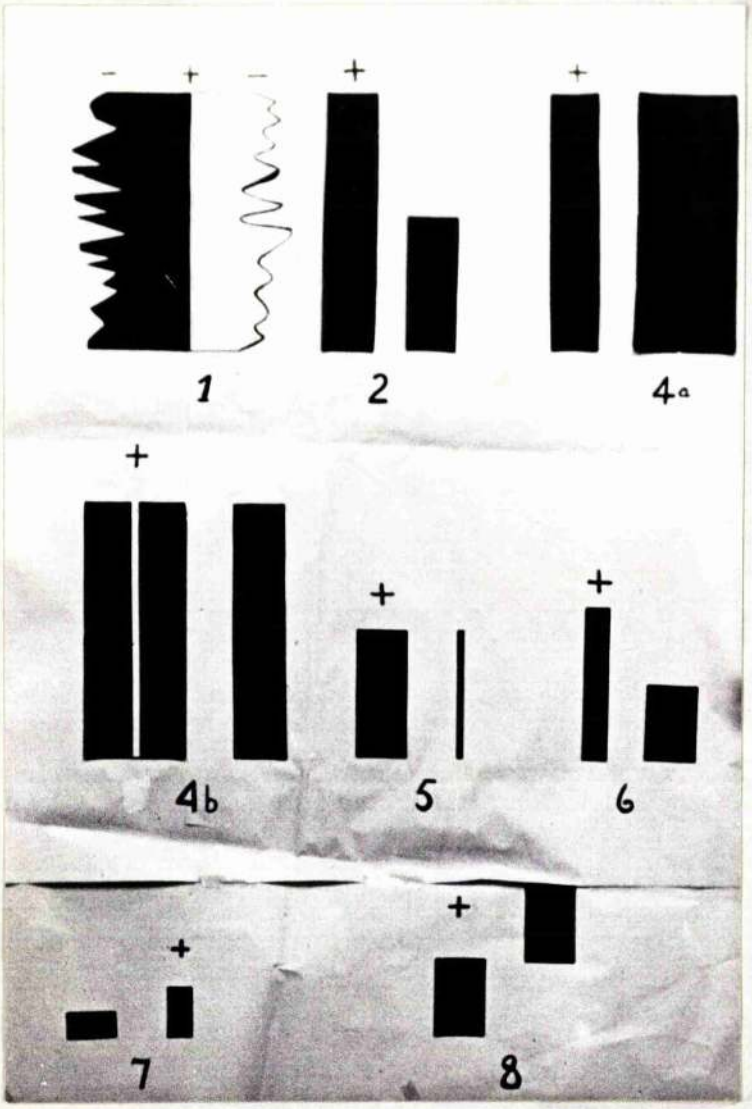


Fig. 2a.

Fig. 2a and 2b: diagram summarising the results of form perception experiments with locust nymphs. The numbers refer to the numbers of the experiments in the text and the + indicates the preferred figure of each pair.

NOTE All figures were of a uniform and equal black. In some cases they do not appear so because of the lighting of the photograph.

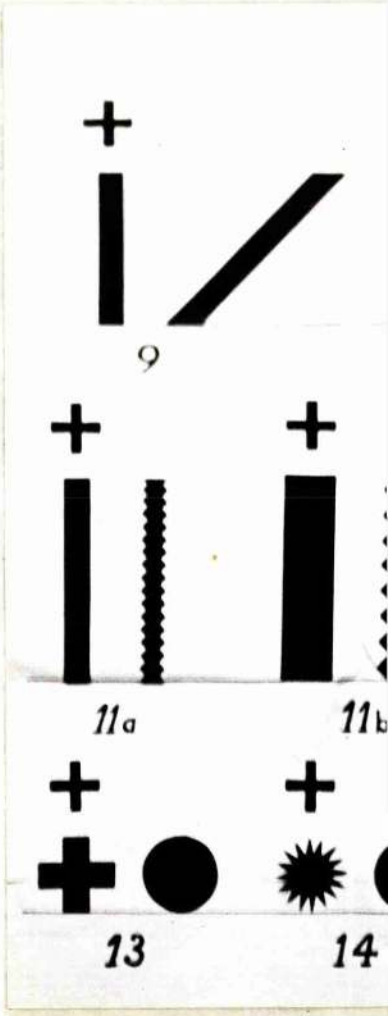


Fig. 2

ommatidia are stimulated cannot be determined from this experiment.

The importance of a vertical straight edge as opposed to an oblique straight edge.

Experiment 9. Vertical stripes and oblique stripes.

Forms. Straight black stripe 6" tall by 1" broad placed vertically. Long black stripe 1" broad at 45° to the vertical. The length of this stripe was such that the top of the stripe was a vertical distance of 6" above the floor, i.e. the same as the vertical stripe. The oblique stripe was of course greater in area and perimeter than the vertical stripe. The pair of figures are as in fig. 2

Readings. Since the animals could be orientating to any part of the oblique stripe and not just to the part near the floor it was decided to score an animal as being attracted to an oblique stripe if it reached the wall at any point within the 6" horizontal distance delimited by the projection of the oblique stripe on the floor. Since the vertical stripe was only 1" broad the insects had, on the basis of chance, 6 times the chance of reaching the oblique stripe as of reaching the vertical stripe.

Animals. 5th instar, phase gregaria. 12 animals tested each 5 times.

Results. These are given in table 11. The animals showed a highly significant preference for the vertical stripes.

Conclusion. It is clear from this experiment that a vertical straight edge is more attractive to these insects than an oblique edge

at 45° notwithstanding the fact that the latter object has the same vertical height as the former and a greater area and perimeter.

The importance of a straight vertical edge.

The ~~verticalness~~ verticality of the edge had been shown to be important (previous experiment) the distance from the ground (position) only important in a negative sense (expt. 8). There remained the question of the straightness of the edge. Experiments 10 and 11 tested this.

Experiment 10. Straight stripes and wavy stripes.

Forms. Straight black stripe, 1" broad and 8" high. Wavy black stripe 1" broad and 8" vertical height. (Note both figures have the same vertical height). The pair of figures used are shown in fig. 2b.

Animals. 5th instar, phase gregaria. 20 animals each tested 5 times.

Results. These are given in table 12.

Conclusions. These are given below along with the conclusions of expt. 11.

Experiment 11. Straight stripes and serrated stripes.

The objects used in these tests are shown in fig. 2b.

11a. Forms. Straight black stripes 8" tall and 1" broad. Serrated black stripe 8" tall and 1" maximum breadth. The details of the serration can be seen from the figure.

Animals. 5th instar, phase gregaria. 40 animals each tested 5 times.

Results. These are given in table 13a.

Conclusions. See below.

11b. Forms. Straight black stripe 2" broad, 8" high. Serrated black stripe ($2\frac{1}{2}$" maximum breadth) 8" high. Both stripes had the same area - 16 sq.".

Animals. 5th instar, phase gregaria. 11 animals, each tested 5 times.

Results. These are given in table 13b.

Conclusions. See below.

Experiments 10 and 11. Conclusion. In both tests the insects showed a preference for the straight stripes. This was not so marked in the first test (11a) as in the second (11b) hence the larger number of animals required in the former to obtain significance.

It is quite clear from these experiments that a straight vertical edge is of overwhelming importance as a figural quality as far as these insects are concerned. Although the serrated and wavy figures both possess larger contours than the straight stripes, neither of these figures is as attractive as the stripe with the equivalent straight vertical edge. This point is of great importance in considering the basis of form perception in these insects and will be discussed more fully later.

The question of the importance of area did not enter into these experiments, for in experiment 10 the wavy stripe was of greater area than the straight, in experiment 11a the serrated stripe was of smaller area than the straight, while in experiment 11b the serrated stripe was of exactly the same area as the straight.

Although it is possible that the serrations of the figure in experiment 11a were so small as to merely render the figure edge blurred

to the insects, nevertheless, there can be little doubt that the serrations in 11b were quite distinct to the animals. It may be for this reason that the results of the latter experiment are more clear-cut than those of the former.

The possibility of an I.R.M. for a straight vertical edge.

The great importance of a straight vertical edge, as shown above, suggested that the locust nymphs in question might possess an innate attraction to straight vertical edges as compared to all other sorts of edge, i.e. that vertical edges operated as an Innate Releasing Mechanism (Tinbergen 1951) releasing the approach response in these insects. If this were indeed the case it might be found that, within limits, the attractiveness of a straight vertical figure could not be compensated for by an increase in any of the other figural properties previously shown to be important.

The hypothesis was tested in the following way (expt. 12).

Experiment 12. Short straight vertical stripes/tall serrated stripes.

Forms. Black rectangle 4" tall, 2" broad. Black serrated figure 8" tall, $2\frac{1}{2}$" maximum breadth. (see fig. 2b.). The tall serrated stripe was twice the area of the short stripe and had a much longer perimeter.

Control. This was performed with vertical straight and serrated stripes of equal height (8"). (Figures as in expt. 11b).

Animals. 5th instar, gregarious phase; 15 animals each tested 5 times in the control and in the experiment.

Results. These are given in tables 14a and 14b. The insects showed a preference for the tall serrated stripes. The controls showed that when the straight and serrated stripes were the same height the straight ones were chosen as had been found previously (expt. 11b, table 13b).

Conclusion. This experiment demonstrated that, if there were an I.R.M. for a straight vertical edge, its effect could easily be out-balanced by increased tallness of the opposing figure. It may well be, of course, that the complete I.R.M. is "tall straight vertical edge".

Experiment 13. Cross against circle.

One of the pairs of figures used by Hertz in her experiments was a circle and a cross and it was found that bees could distinguish the one from the other. It was decided to perform the same test with the locust nymphs.

Forms. Black cross, limbs 1" wide, overall width and height 3". Upright. Black circle (3" disc) 3" diameter. The figures used are shown in figure 2b..

Animals. 5th instar, phase gregaria. 20 animals each tested 5 times.

Results. These are presented in table 15. In this test the insects showed a significant preference for the cross ($p < .01$).

Conclusion. It is realised, of course, that this test only shows that the insects can distinguish between these figures. Since the figure of the cross contained the added complication of vertical edges nothing could be concluded about the importance of the other property, namely,

articulation. The importance of this property was studied in the final experiment.

The importance of articulation.

Hertz found that the amount of articulation or breaking up of the contour of a figure was an important property affecting its attractiveness. It was decided to test this in the case of locust nymphs. While it is true that experiment 11 had shown a broken-up edge (serrated) to be less attractive than a straight vertical edge, nevertheless it was thought possible that, in the absence of a straight vertical edge, articulation might be an important figural quality. This was tested as follows.

Experiment 14. Circle against an 8-pointed and 16-pointed star.

Forms. Black circle (disc) 3" diameter. 14a. Black 16-pointed star, outside diameter 3". 14b. Black 8-pointed star, outside diameter 3".

Animals. 5th instar, phase gregaria, in both cases. 14a. 20 animals each tested 5 times. 14b. 12 animals each tested 5 times.

Results. These are given in tables 16a and b. In each case the animals showed a significant preference for the star.

Conclusion. From this experiment it can be concluded that articulation is an important quality influencing the attractiveness of a figure. In the absence of vertical components the more articulated figure is the more attractive.

Discussion.

From the present investigation two principal facts have emerged. Firstly, that, without any previous training, nymphs of the Desert Locust are spontaneously attracted to figures in the environment and to the contour lines of these figures. Secondly, there is a spontaneous preference for some figures as opposed to others showing that, under these conditions, the insects can discriminate between these figures.

Hertz (1935) believed that such discrimination ability would be found in all insects with good vision. Whether or not this is true it is interesting to compare the results of the present experiments with those obtained by other workers for other insects.

The results of the present investigation are summarised pictorially in fig.21., and it will be found useful to consult this figure in conjunction with the discussion in the text.

The first experiment (expt. 1) showed that the locust nymphs were attracted to black/white boundaries. A similar result was obtained by Kalmus (1937) with Dixippus morosus and he called the reaction "photo-horo-taxis". It has also been demonstrated in the larvae of the Sawfly Dolerus palustris (Wallace 1954). Williams (1954) in his experiments with grasshoppers also noted the attraction to black/white edges although he wrongly called this skototaxis (see Fraenkel and Gunn 1940). The attraction of the caterpillars of Lymantria monacha to the edges of very broad blue objects on a white background is almost certainly the same

response (Hundertmark 1937 b).

The importance of the contrast of figure edges as shown in experiment 3 where black stripes were preferred to grey stripes has also been demonstrated in bees (Hertz 1931), in caterpillars (Hundertmark 1937 a) and in stick insects (Hundertmark 1937 a). It is also the reason for bees being attracted to the object with the darkest shadow (Hertz 1931).

The preference for the taller of two stripes (expt. 2) is also shown by lepidopteran caterpillars (Hundertmark 1937 b).

Experiments 4 and 5 showed that there was a certain intermediate breadth of stripe which the nymphs preferred to either a very broad stripe or a very narrow stripe. Hertz (1929b) found that with black articulated figures of median sizes there was a slight preference for the smallest and that this preference was very strong in the case of black discs (if the smallest was not too small to be seen). Hundertmark, however, found that his caterpillars preferred the broadest object present when the objects were of equal height. Williams (1954) found that grasshoppers showed no preference for any particular breadth of stripe, but since he used breadths ranging only from 2 - 18 mm. (as against .25", 2", 4" in the present case) it is very possible that his stripes were not broad enough to show the same effect as was seen in the present tests.

The results of experiment 7 showing the importance of vertical objects as against horizontal objects is in agreement with the results obtained by Williams for grasshoppers (1954). According to Buddenbrock (1935) Eristalis shows a slight preference for horizontal stripes as

compared with vertical stripes.

The ignoring of the higher of two objects if it is at too great a distance above the floor (Expt. 8) is exactly what Hundertmark found in his experiments with caterpillars (Hundertmark 1937 b).

The ability of locust nymphs to discriminate between a vertical edge and an oblique edge and their preference for the former (expt. 9) is shared by the caterpillars of Lymantria monacha (Hundertmark 1937 b). In his work with grasshoppers, however, Williams (1954) found no preference for a vertical stripe as against an oblique stripe at 45° (the angle of inclination in the present tests). This is difficult to understand in view of the fact that he also found vertical stripes to be preferred to tall narrow triangles with sides inclined at only 5° to the vertical.

Straightness of the vertical edge was demonstrated to be an important feature of a figure (expt. 10). The only comparable experiment in the literature appears to be that of Williams (1954) who found, contrary to the present results, that straight stripes and a vertical zigzag of stripes were equally attractive to grasshoppers.

Bees differentiate a cross from a circle (Hertz 1929a). Bees (von Frisch, 1914; Baumgärtner, 1928; Hertz 1929 etc.) and Butterflies (Ilse, 1932) prefer an articulated figure to a circle. In each of the experiments 13, 14a and 14b the same was found to be true of the locust nymphs tested.

One of the central problems in any consideration of form discrimina-

tion is the analysing of the attractive qualities of the figures used. Knowledge of these properties then yields information as to the basis on which the discrimination is made for it explains why one figure is more attractive than another or can be differentiated from it. By far the greatest contributor to the knowledge of form discrimination in insects is Hertz (see list of references) who made a detailed study of the problem in bees. She believed that the attractiveness of figures for bees was not due to their resemblance to flowers, for other figures could be constructed which were not found in nature but which were even more attractive than those which were (Hertz 1929b). She thought that there were certain properties of a figure which made it spontaneously attractive to bees. An exaggeration of these in the "unnatural" figures mentioned above made them more attractive than "natural" ones which also possessed these qualities but to a lesser extent. She also thought it possible that similar equally spontaneous choices might exist in other arthropods with different living requirements. If this were so it would strengthen the idea that the response to such figural qualities was a general property of a simple nervous system (Hertz 1929b). For this reason it is necessary to consider her work in more detail and to compare it with the few deductions which can be made from the present experiments.

During the course of her study Hertz performed a long detailed series of experiments embodying numerous results and tentative hypotheses.

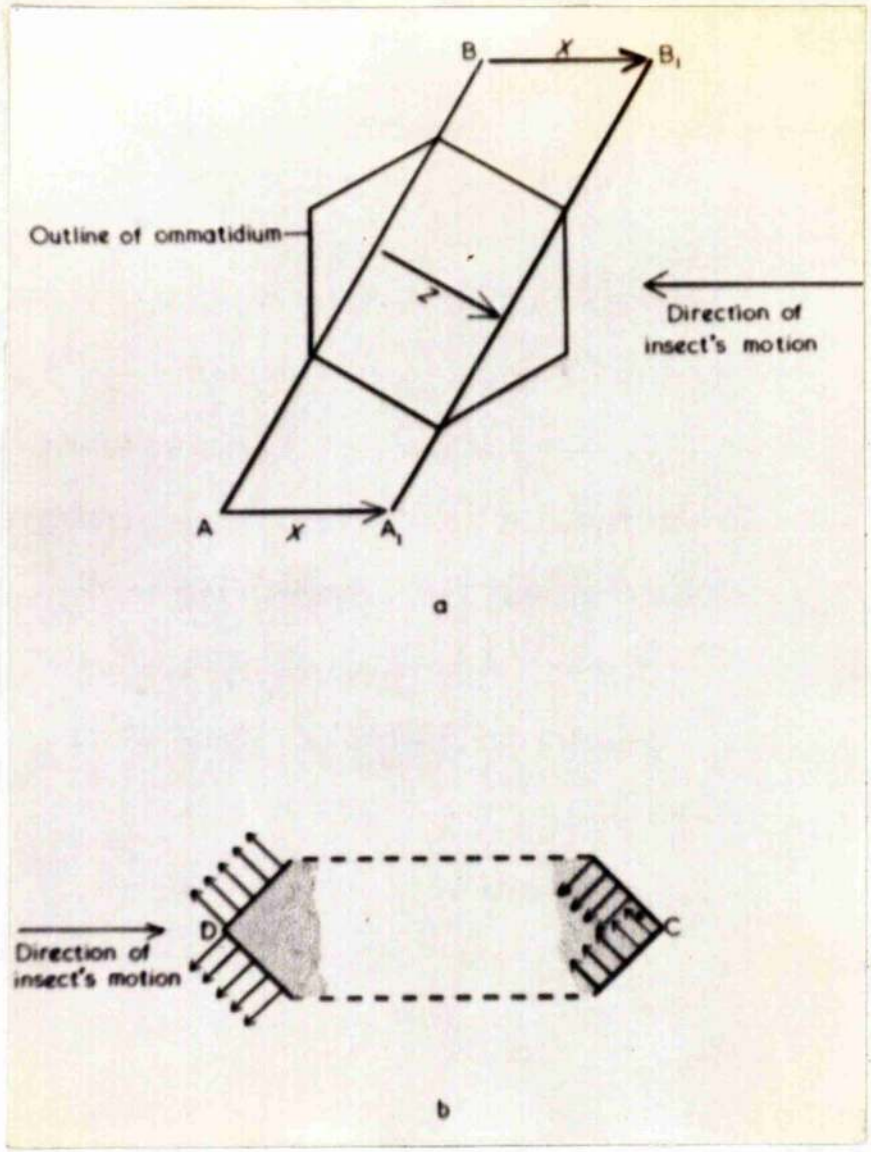


Fig. 3.

Diagram illustrating Hertz's idea of convergence and divergence of contour lines.(See text p. 39).

3a – AB is part of the contour of a figure moving to A'B'. x is the direction of movement of the pattern as a whole with respect to the insect.
Z is the apparent direction of contour movement across an ommatidium, Note this is at right angles to the contour and is not in the same direction as the movement of the whole pattern.

3b – The convergence and divergence of lines of stimulation as an insect passes a pattern with a serrated edge. (The same effect will be produced by a wavy edge). The small arrows indicate the apparent direction of contour motion(cf. Z in 3a).Points D and C are points of divergence and convergence respectively.

From her writings it is difficult to disentangle her final conclusions but a reasonable interpretation of them would appear to be as follows. Her hypothesis is expressed in terms of the transitory stimulation of ommatidia produced by the movement of the figure contours over the eye. She differentiated two main classes of figural properties which determined a figure's attractiveness and on which figures were differentiated. These were "figural intensity" and "figural quality" (Hertz 1933). Figural intensity was related to contour richness which in turn was related to the contour length, the degree of articulation (disruptiveness of the contour), the nearness of the contours to one another (relative smallness of the figure) and to the amount of contrast with the background (Hertz 1929b). Figural quality in the case of bees was found to be related to the angle of the contour lines to one another. When contour lines at an angle to each other pass over the eye the apparent direction of motion is at right angles to each contour line and hence the waves of stimulation produced by the contours will diverge or converge (see fig.3 for a full explanation of this).

To make the distinction clearer, Figural intensity is measured quantitatively in terms of the number of ommatidia stimulated in a given time as the image crosses the eye. Figural quality depends on the actual angle of the contour lines to one another, i.e. to the order in which the ommatidia are stimulated and the spatial relationship between the groups of ommatidia stimulated. Hertz considered that the tendency of

the contour lines to run back on one another (as in a small circle) was an important attractive feature of a figure. It is true that the angle of the contours to one another must be correlated with the degree of articulation but Hertz thought that the divergence or convergence of the contour lines had a special significance apart from the mere increase in contour length achieved by articulation.

Hertz showed that bees did not merely respond to the total number of stimulus changes caused by the movement of the contours over the eye (1931 and 1935).

Other workers who investigated the basis of form discrimination in bees were Wolf and Zerrahn. These authors strongly maintained that Hertz was wrong and that the number of stimulus changes per second as the bee flies over the pattern is the important measure of the attractiveness of the figure. It has indeed been shown that bees are attracted to flicker (Wolf, 1934; Wolf and Zerrahn-Wolf, 1934). It was claimed that there was a spontaneous choice of figures which was strictly according to their richness of contour. There was a straight line relationship between % choice (i.e. number of times out of the total that a pattern is chosen spontaneously from all the others when they are presented together) and contour length/black area (Zerrahn 1934). For patterns of the same area the choice is directly proportional to the contour length. For patterns of the same degree of coarseness the choice is always in favour of the pattern of greatest area (Wolf and Zerrahn-Wolf, 1934). These workers therefore concluded "that recognition and distinction of patterns

by bees is based upon the transitory stimulation produced by a pattern and that the pattern as such is of no importance" (Wolf and Zerrahn-Wolf 1936).

Hertz (1931 and 1935) strongly denied that the attraction to flicker was the complete explanation of form discrimination in bees.

Ilse (1932) found that for butterflies there was a spontaneous choice of the figure with the greatest contour richness (i.e. length of contour/extent of figure).

The present investigation has not been detailed enough to allow of the putting forth of a complete hypothesis to explain the basis of form discrimination in locusts. To do so would require the further testing of small positive figures against large negative figures in order to investigate further the effect of shape independent of size (this has been done in one test, expt. 12). Furthermore, the technique of spontaneous choice experiments has the following disadvantage. Although Zerrahn (1934) has stressed that training to a figure is only possible if it coincides with the normal spontaneous choice, nevertheless, in a spontaneous choice experiment, a difficulty would arise when the two figures were almost equally attractive, since, without secondary reinforcement (~~to food training~~ e.g. training to food) the animal would not be forced to try to discriminate between them. An equal attraction to each object in such a case would not mean, therefore, that the insects could not discriminate between them.

It is, however, interesting to see just how far the present results

are explicable on the theories of Hertz or Zerrahn. Can they be explained solely on the basis of the frequency of stimulus changes/unit time (Zerrahn) or are there additional factors as Hertz believed? It will be found that, although the present results are not greatly detailed, nevertheless they are sufficient to show certain discrepancies from what would be expected on the basis of these theories.

Zerrahn (1934) stressed the importance of the direction in which bees flew over a striped pattern. If the bee flies parallel to the stripes there are the minimum number of stimulus changes per second and if it flies at right angles to the stripes there are the maximum number of changes per second. The same will of course apply to an insect which is crawling horizontally; the vertical contours will move fastest over the eye and produce the greatest stimulation (the horizontal contours will move much more slowly up or down the eye as the insect approaches or retreats from a figure). Bearing this important fact in mind and also the fact ~~present~~ present that the experiments clearly demonstrated the importance of the vertical edge, it can be seen that the results of the experiments 1 - 8 are immediately explicable. Those figures with the longest vertical edge will give the most stimulation (expts. 2, 6, 7). Further, the greater the distance between the vertical edges (e.g. the broad objects in expt. 4a) the fewer the number of stimulus changes per second as these edges cross the eye. There will be a greater interval between the stimulation of an ommatidium by one edge and its stimulation by the

second edge than there would be for a narrower stripe (expt. 4a). Hence the addition of another two vertical black/white contours to a very broad figure would make the figure more attractive (the result of expt. 4b). The explanation of the result of experiment 5 is probably that the narrow strip was so narrow as to be seen indistinctly.

Objects with the same vertical edge and the same breadth (expt 8) will provide the same stimulation. In this experiment the apparent preference for the lower object is probably due to the animals' failing to find something to orientate to when they approach very close to the higher object (see the conclusion of this expt. p.27).

So far, then, these results are completely explicable either on the theory of Zerrahn or on that of Hertz, since they conform to the latter's ideas of <u>figural intensity</u> (p.38) and do not involve figural quality. The same applies to the experiments 12, 13 and 14, the longer vertical contour in 12 giving greater stimulation than the contour of the other figure and the articulated figures giving more stimulation than the plain circles.

The results of experiments 9, 10 and 11 are <u>not</u> explicable on <u>either theory</u>. Oblique stripes give less stimulation than vertical stripes because of their angle but this is compensated for by their increased length (this applies to stripes ranging from the vertical up to 30° to the horizontal. (See Hertz 1934a). Since, in experiment 9, the oblique stripe was inclined at 45° and was arranged so as to be the same vertical height as the vertical stripe, it should provide the same stimulation as this latter figure. Yet the vertical stripe is chosen. In

this case, therefore, the choice is not made simply on the basis of the total frequency of stimuli/sec. as Zerrahn suggests. The same argument applies to the experiments 10 and 11 for the serrated and wavy edges can simply be looked upon as a succession of oblique edges (the serrations were at angles of 45° and the inclination of the wavy edge was more than 45° to the horizontal. Hertz's theory also fails to explain these tests for in experiments 10 and 11 the wavy and serrated edges should give numerous points of convergence or divergence of stimuli (see p.38-39) and hence should possess a greater figural quality than the vertical edges.

From the present experiments, therefore, it can only be concluded that, apart from a discrimination based on the number of stimuli/second and reflected in the importance of figures with vertical edges and of articulated figures, there is a further preference for stimulus changes which occur in vertical rows (as arising from a vertical edge) as compared with oblique rows of ommatidia responding together (as to an oblique, wavy, or serrated edge). This could be called an I.R.M. for a tall straight vertical edge (although this explains nothing). When there is no vertical edge (expt. 14), or where it is too small (expt. 12), the discrimination would be made purely on the basis of the number of stimuli/second.

Experiment 12 shows that the importance of the straight vertical edge can be outweighed by a preponderence of some other property in the contrasted member of the pair. This is to be expected since both Hertz (1931, 1934c) and Wolf and Zerrahn-Wolf (1934) found that different

figural properties could be balanced against each other.

It is possible that the preference for a vertical edge may be found in many crawling insects which climb on stems. Further, it is possible that the mechanism in the central nervous system for performing the discrimination is a relatively simple one, since, as mentioned above, lepidopteran caterpillars possessing only 6 pairs of ocelli are able so to discriminate.

PEERING.

Introduction.

From time to time, locust nymphs, previously walking, will halt and then perform side to side swaying movements of the anterior part of the body. This is accomplished by straightening the first and second legs on one side and bending the corresponding members on the other side. The hind legs are seldom involved and none of the six feet are moved. By stretching the left legs for example, and bending the right, the body is made to sway to the right. During this side to side movement the body and the head are not tilted, the vertical axis of the head remaining perpendicular to the ground.

This response was first commented upon by Kennedy (1945) who observed it in the field and used the term "peering" to describe it, believing that it was an optical response. Ellis (1953) agrees with this. Chapman (1955) however, regarded its significance as "doubtful" since he had observed that it sometimes occurred in a uniform visual field.

As already stated, (p.14) such peering had been observed during the course of the form perception experiments, when the insects were orientating to the object and this strongly suggested that it was indeed a visual response. The response was therefore investigated in more detail.

Method of Measuring Peering Angles.

The instrument used for measuring the angle through which a locust's body moved during peering was a protractor with a moveable pointer. The whole was made of perspex, the pointer being a broad section of perspec with a fine line etched on it. (The breadth of the sector allowed the animal to be viewed through it without distortion.

The instrument was held horizontally above and slightly behind the animal. The longitudinal axis of the animal's body was a line with the 0^{o} line on the protractor. In peering, the insect moves the whole body except the posterior tip of the abdomen wh ch rests on the ground, so that the head, in swaying traverses a horizontal arc whose radius equals the body length. The centre of the protractor, i.e. point of attachment of the pointer, was visually superimposed on the tip of the abdomen. When the animal's body moved the pointer was moved by hand to follow it, keeping the line of the pointer on the longitudinal axis of the body. The peering angle in degrees was read off from the protractor scale.

During the experiments the instrument was held approximately one foot above the animal and behind it, in which position it did not disturb the animal. Trial measurements made of unknown angles drawn on paper had shown that, at the distance stated above, accuracy could be

obtained to within one degree.

Peering - a Visual Response.

Experiment 1.

If peering were a movement correlated with the visual sense, it should be possible to show that it was influenced by altering the position of objects in the visual field. This was the principle upon which the following experiments were based, the animals being presented first with an object in front and secondly with an object at the side, and measurements of the peering angles being made in each case.

Apparatus and Method. The apparatus used was a white walled, white floored arena (2 ft. diameter) with a single tall black stripe (10" tall by 2" broad) stuck on the wall of the arena with its base on the floor. Lighting was from an overhead source and thus, apart from the black object, the visual environment was otherwise uniform. The insect to be tested was then placed at a certain distance and angle from the black stripe. It was of course imperative that the animal be confined to one point so that the distance and bearing of the object from the animal's position could be known accurately. This was achieved in the following way.

It was found that if a fifth instar nymph were placed on a small narrow platform like a diving board it would walk along to the end, sit quietly and peer. By suitable placing of the board in the arena the animals could thus be positioned at a known distance and angle to the

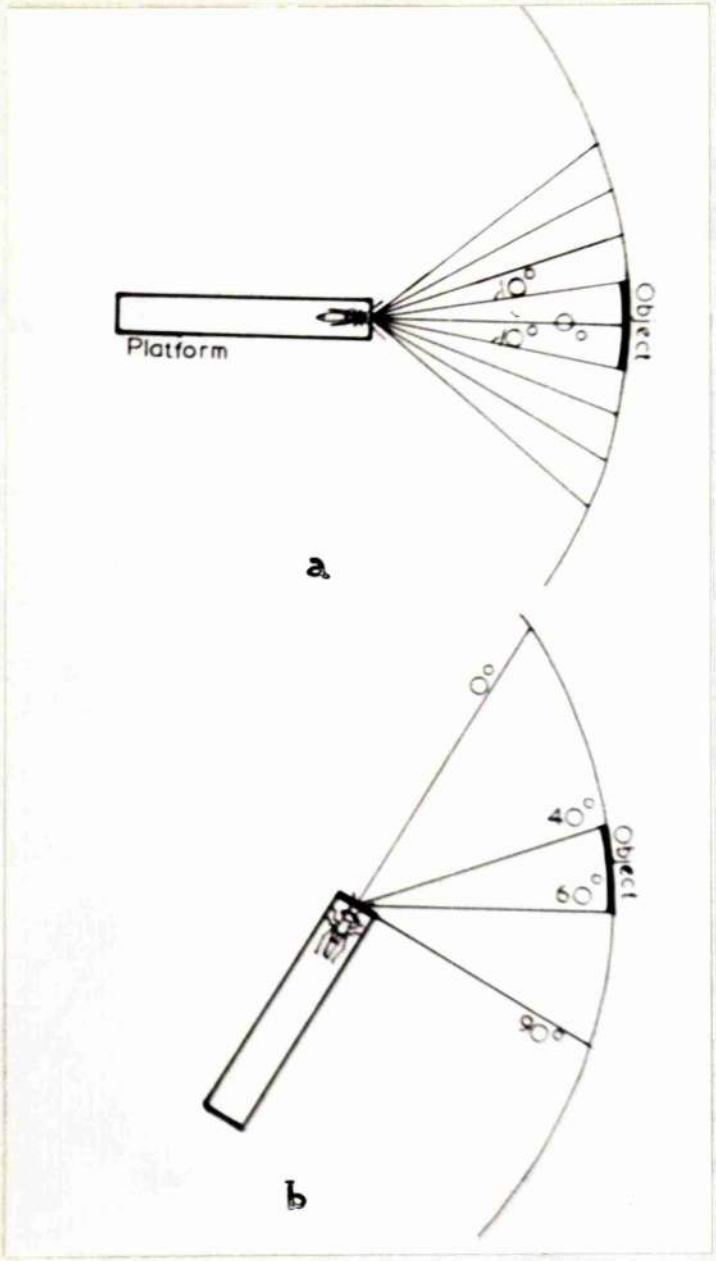


Fig. 4.

Plan view showing relative positions of "diving board"and object in the two experimental conditions
a - object in front (10° left and 10° right).
b - object at the side(40° - 60° right).

black object. The "diving board" was 1" wide, 6" long and raised 2" off the floor.

The longitudinal axis of the diving board was taken as the line of bearing 0° (since almost all animals settled with their bodies along this line) and corresponding reference lines were drawn on the floor at intervals of 10°.

Animals. In these tests 5th instar nymphs were used since their large size facilitated measurement of the peering angle.

Object in front. (Fig. 4a). In this test the board was placed so that the black stripe was directly in front of the insect at a distance of 6" away. At this distance the stripe subtended a horizontal angle of 20° and thus, when placed symmetrically on the 0° line, its vertical edges lay 10° to the right and left respectively.

The animal to be tested was placed on the board; it then walked to the end, settled and peered and the peering angles were measured in degrees to the right and left of the mid line. In almost all cases the animals settled with their longitudinal body axis on the 0° line. In the few cases where this was not so the results have been omitted.

Object at side. (Fig.4b). In this test the arrangement was such that the object lay at an angle of 40-60° to the right of the animal. As in the first test the distance from the object was 6". The procedure was the same as described above and the peering angles were noted.

Results. The results obtained are presented in Tables 17 and 18

Fig. 5.

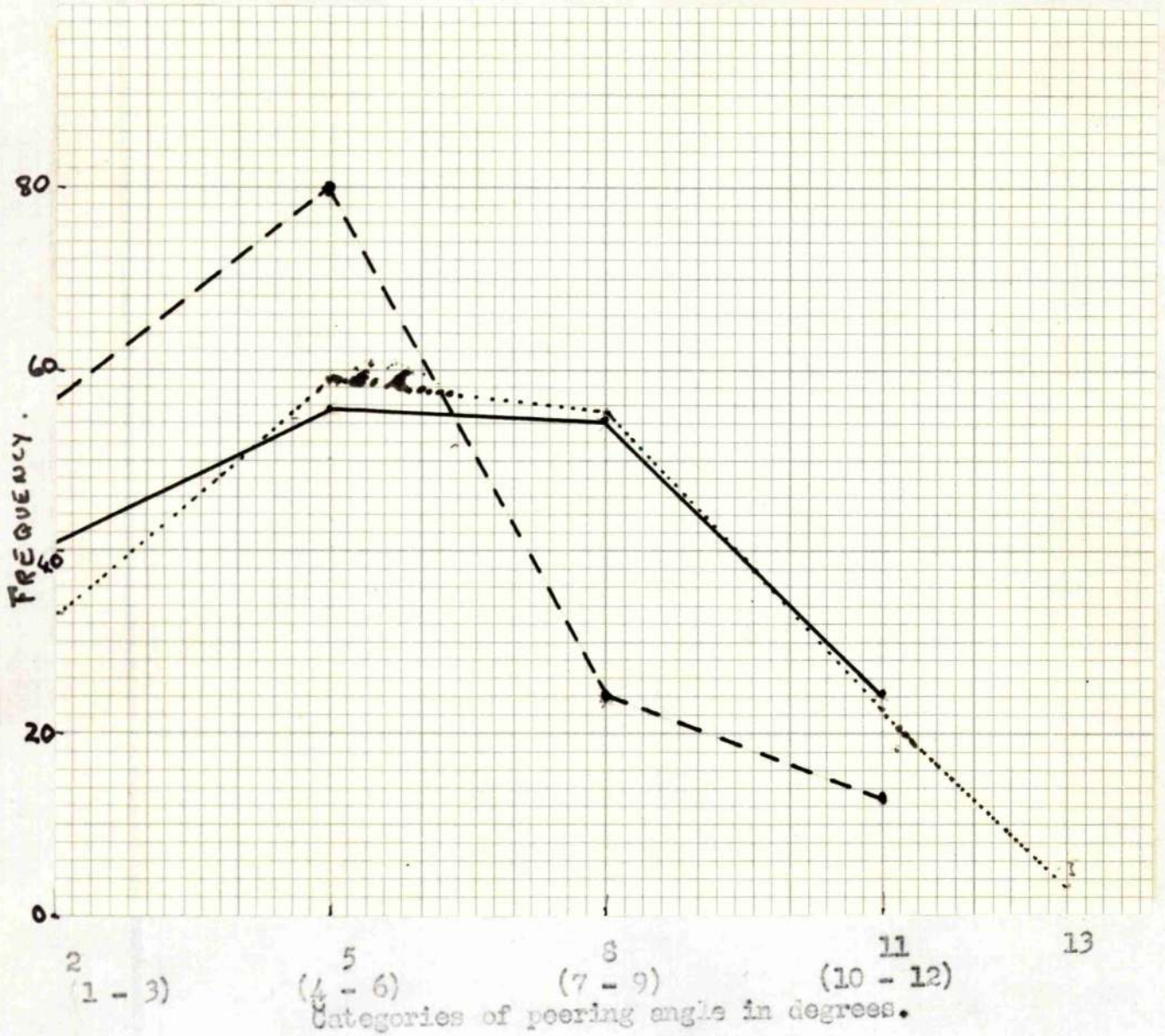


Fig. 5.

Graph showing distribution of peering angles of various sizes (irrespective of whether to right or left) in three situations

– – – object subtending 20° directly in front of insect.
——— object 40° - 60° to the right.
..... objects all round.

Fig. 6.

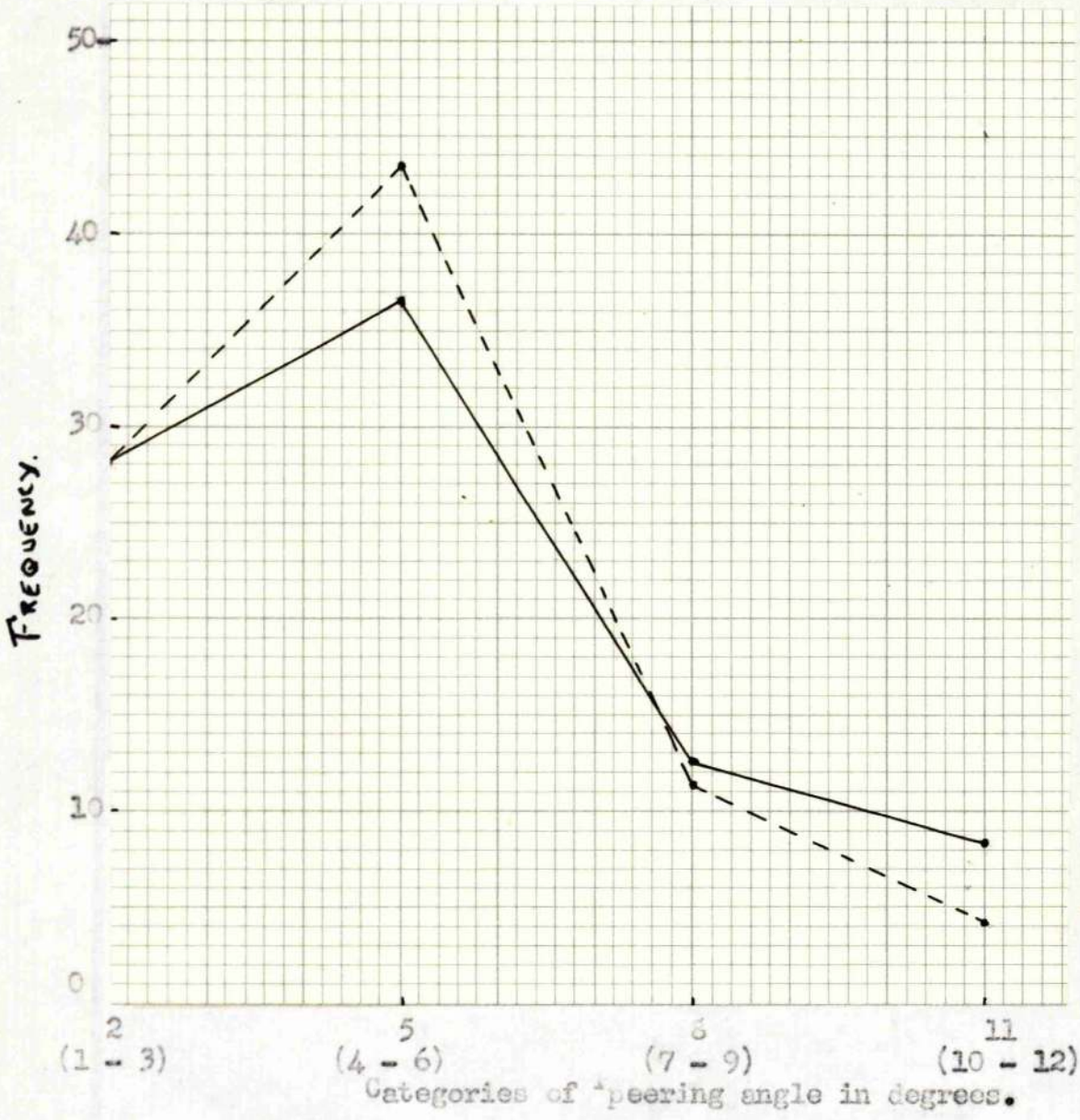


Fig. 6.

Graph showing distribution of peering angles of various sizes in the situation where there is an object subtending 20° directly in front of a locust nymph.

--- angles to the left.
—— angles to the right.

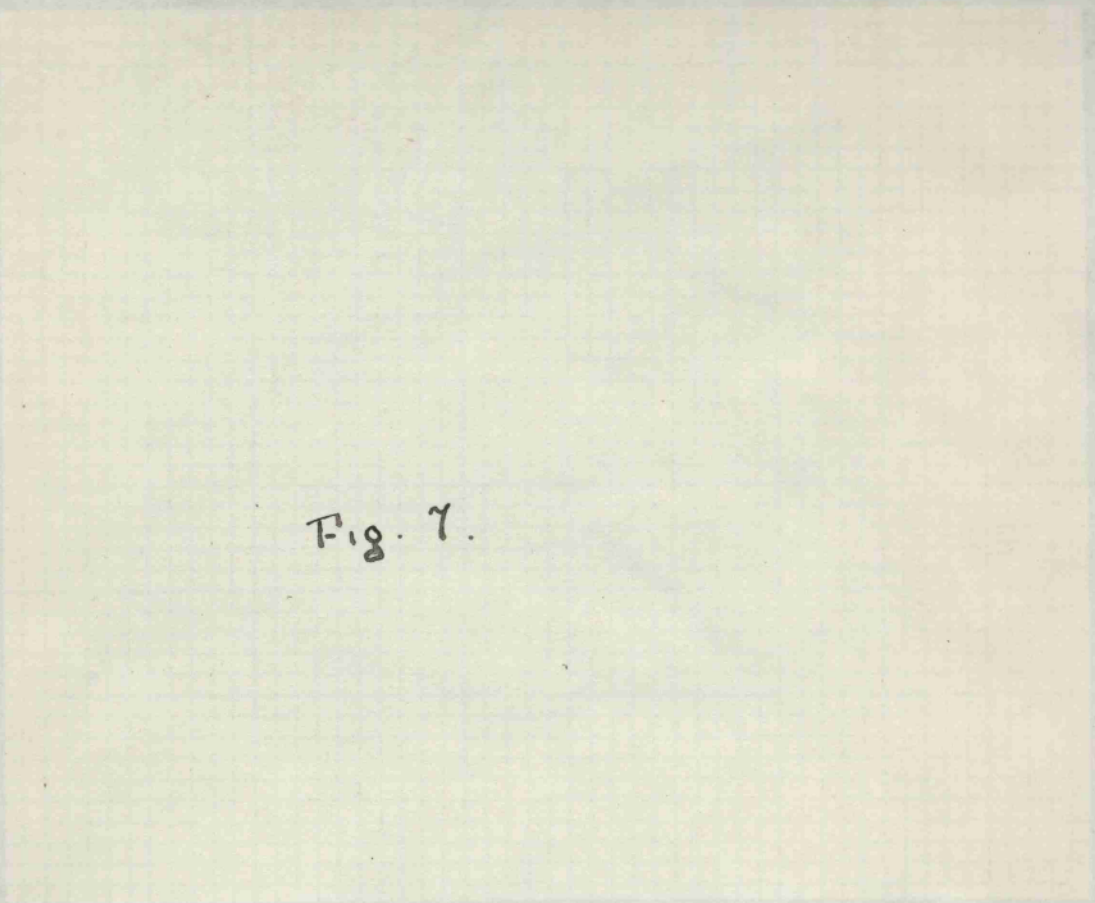


Fig. 7.

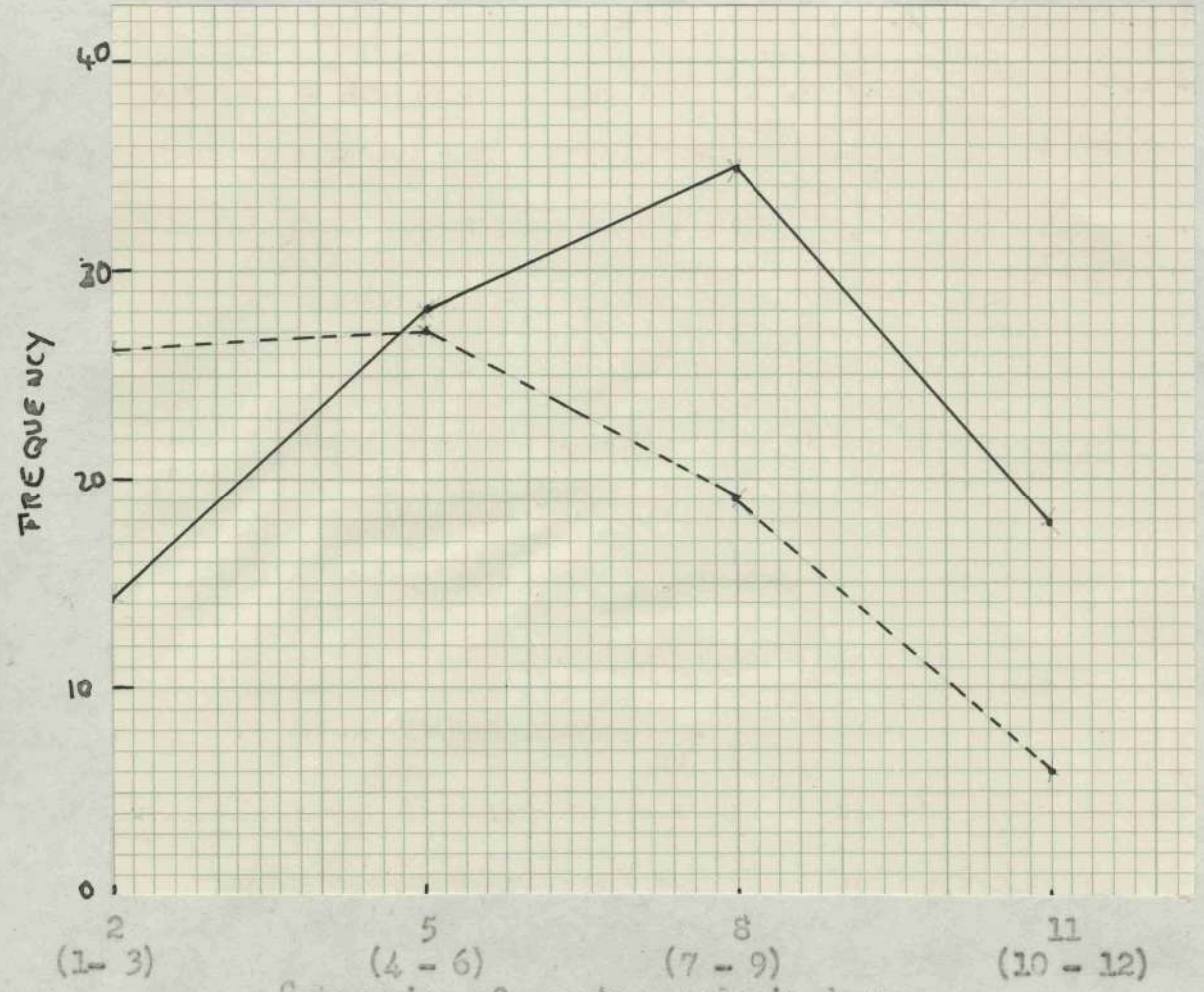


Fig. 7.

Graph showing distribution of peering angles of various sizes in the situation where there is an object lying 40° - 60° to the right of a locust nymph.

--- angles to the left.
——— angles to the right.

The angles of peering recorded varied from 1-12°. For convenience, they are divided into four categories, angles of 1-3°, 4-6°, 7-9°, and 10-12° The frequency with which angles in these groups occurred is noted and also whether these were peering angles to the left or right of the mid line (long. axis of the insect). Since the animals do not always peer the same number of times, the total number of readings is slightly different in each case. In Table 17 the total number of readings = 123 and in Table 18 173. To facilitate comparison between the results in these tables the results in Table 18 are multiplied by 1.4 (i.e. ratio 173/123) so as to bring both populations to a value of 173 results. The corrected values are listed in Table 17, foot. In all graphs these corrected values are used.

Fig. 5 In this graph the total frequency of occurrence of angles in each group is plotted irrespective of whether they are to right or left. This is done for both situations "object in front" and "object at the side".

Fig. 6 In this graph the frequency of different sized angles to right and left is plotted for the situation where the object is in front of the animal (10° left, 10° right).

Fig. 7 As in the previous graph the frequency of different sized angles to right and left is plotted. The object being at 40-60° to the right of the animal.

Discussion.

From the Graph (Fig. 5) these following points can be made. The maximum angle of peering recorded is about 12°. In both cases, i.e., "object in front or at the side, angles of peering between 4 and 6° are

most common. When the object is in front there is a high proportion of angles 4 to 6° and angles of 7-12° are rare. When, however, the object is at the side the distribution is different. Angles of 4-6° are still most common but not significantly more so than those of 7-9°. The frequency of angles of 7-9° is significantly higher when the object is at the side than when it is in front ($p. < .01$).

The graphs (figs. 6 and 7) show the frequency with which certain sizes of peering angle lie to the right or to the left of the mid line. It is at once clear from Fig. 6 that when the object is in front of the animal the distribution to the right is the same as to the left. Fig. 7 by way of contrast, shows the distributions when the object is lying 40-60° to the right. The smaller angles, 1-3° and 4-6° are still distributed equally to right and left, there being no significant difference between the corresponding points., ($.1 > p > .05$, $p > .99$ respectively). The larger angles 7-9° and 10-12° show a marked difference in distribution, there being a significantly greater number to the right, i.e. to the side of the object, than to the left ($.05 > p > .02$ in one case and $.02 > p > .01$)

The complete results may therefore be stated as follows. The frequency of small peering angles is not affected by the position of objects in the visual field. When an object lies in front of the animal most peering angles are small and all angles occur equally to right and left. When, however, the object is at the side, there is a significant increase in the number of large peering angles and most of these lie to that side on which the object is placed. The smaller angles are still

equally represented to left and right.

Since, then, the position of an object in the visual field influences peering in this way, it can be concluded that the movement of the head called "peering" is certainly correlated with the visual sense. The fact that the smaller peering angles are unaffected by the position of objects in the visual field does not of course mean that the small head movements are not correlated with the visual sense. As will be seen later (p. 66) they are probably small movements used for preliminary visual scanning of the environment.

Peering and Orientation.

It had been noted in the form perception experiments that when peering occurred it was often a prelude to a change in direction. An animal would stop walking, peer, and then walk off in the direction at an angle to the original direction of walking. The following experiment was designed to discover if there were a definite correlation between the peering and the change of direction.

Experiment 2.

Apparatus and Method. The animals were placed singly in the arena on the walls of which were four tall stripes (10" X 2") and four short stripes (5" X 2") equally spaced. Tall alternated with short. The animals were free to walk about the floor of the arena. When peering occurred the peering angles to left and right were noted and the angle of the subsequent track was also measured. When an animal stopped to peer, its longitudinal body

axis was the line of the original direction of walking and the angle of the subsequent track which was measured was the angle between this original direction and the direction taken when locomotion was resumed.

Results. As a criterion for deciding to which side an animal peered most, that side to which there was the largest angle of peering was taken. Since the accuracy of the instrument was only to within 1° the only results used were those where the difference was at least 2°. A typical result is given below:

Body angle to previous track	Peering in degrees Right and Left
0°	3° R., 6° L., 4° R., 7° L.

This therefore represents a "left" peering.

In the first stage analysis, if the subsequent track turned to the same side as that to which there was most peering, the result was scored +ve, if to the other side, -ve. (Note, the angle of the track is not used here). The result of this first analysis was:

Animals	Runs	+	-	p
24	67	52	15	.01

From this it was quite clear that the subsequent track of the animal most often lay to that side where the largest peering angle had been recorded.

A more detailed analysis of the positive was then made, comparing angle of peering and angle of the subsequent track. In cases where the insects peered several times to one side, the average angle of peering is taken. Twelve of the fifty two positives could not be used for the sub-

Fig. 8.

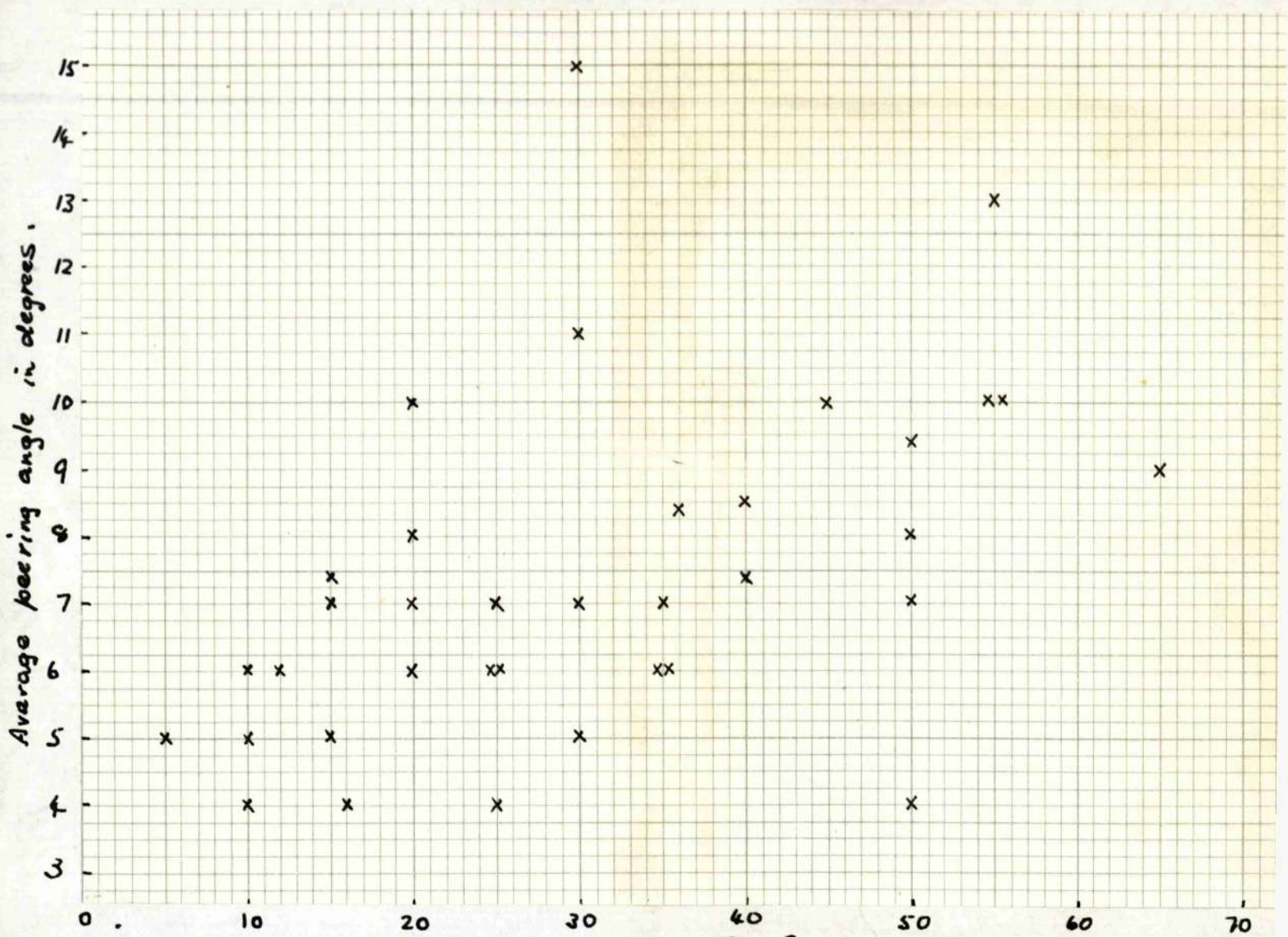
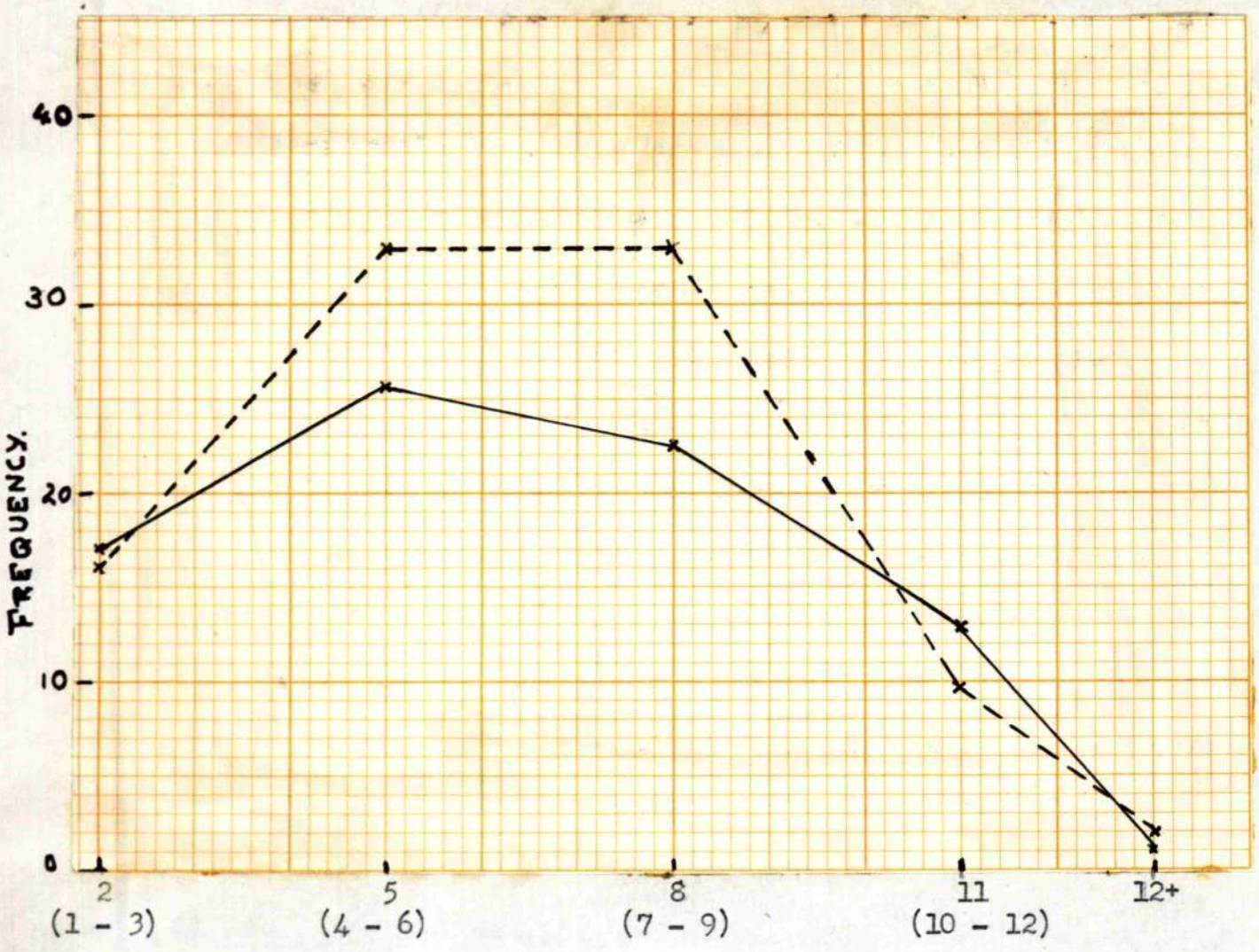


Fig. 8

Scattergram plotting average peering angle a
subsequent track.

Fig. 8a.



Categories of peering angle in degrees.

Fig. 8a.

Graph showing distribution of peering angles of various sizes in the situation where there are objects all round the visual field. (see table 20) Corrected values used.

--- angles to the left
——— angles to the right.

sequent track was very curved and its angle could not be measured. The forty results used in the analysis are presented in Table 19. From this a scattergram was plotted (Fig. 8). The results were analysed statistically and a correlation coefficient calculated which showed a highly significant correlation to exist between average angle of pairing observed and angle of the subsequent track.

Distribution of Peering Angles. The results of this experiment also provide an opportunity of studying the distribution of the peering angles which the insects showed in a visual field with objects all round (i.e. not just 1 object as in the previous experiments).

The results are given in table 20. The corrected values are presented in Fig.5, where they are compared with the results for the 2 previous valuations (object in front, object at the side). The distribution of angles to right and left is plotted in fig. 8a.

Discussion.

As stated above, statistical analysis had shown that there was a highly significant correlation between the angle of peering and the angle of the subsequent track, thus demonstrating the importance of peering as a preliminary to change in direction of locomotion.

From Fig.5 it can be seen that the frequency distribution when there are objects all round is not significantly different from that recorded when there is a single object at the side. In other words when there ar objects all round, the insect seems to spend much of its time

peering at those to the side. As would be expected, however, when there are objects all round, although the animals peer often to the side there is no bias to one side or the other. The distribution of peering angles to right and left are not significantly different (Fig.8a). This contrasts with the situation where there is one object at the side, for in the latter case the larger peering angles are mostly found to the side nearest the object (see Fig.7).

Peering and Distance Estimation.

Introduction.

The previous experiments show that the peering movement is correlated with the visual sense, that it is influenced by the position of objects in the visual field, and that it is correlated with the insect's orientation to these objects. The experiments do not, however, shed any light on the question of the function of peering. What is the insect looking at or measuring from the stimuli received? Both Kennedy (1945) and Ellis (1953) suggest that it "sharpens" vision. As pointed out in the discussion on form perception, the important stimulus for the insect appears to be the transitory stimulation of ommatidia as the image of an object moves over the eye and the above authors suggest that, by peering, the insects can scan the object and produce the requisite image movement. The resulting stimulation would then give more accurate information as to the shape of the object. This hypothesis would be extremely difficult to verify.

However, it was thought possible that peering could also be a means

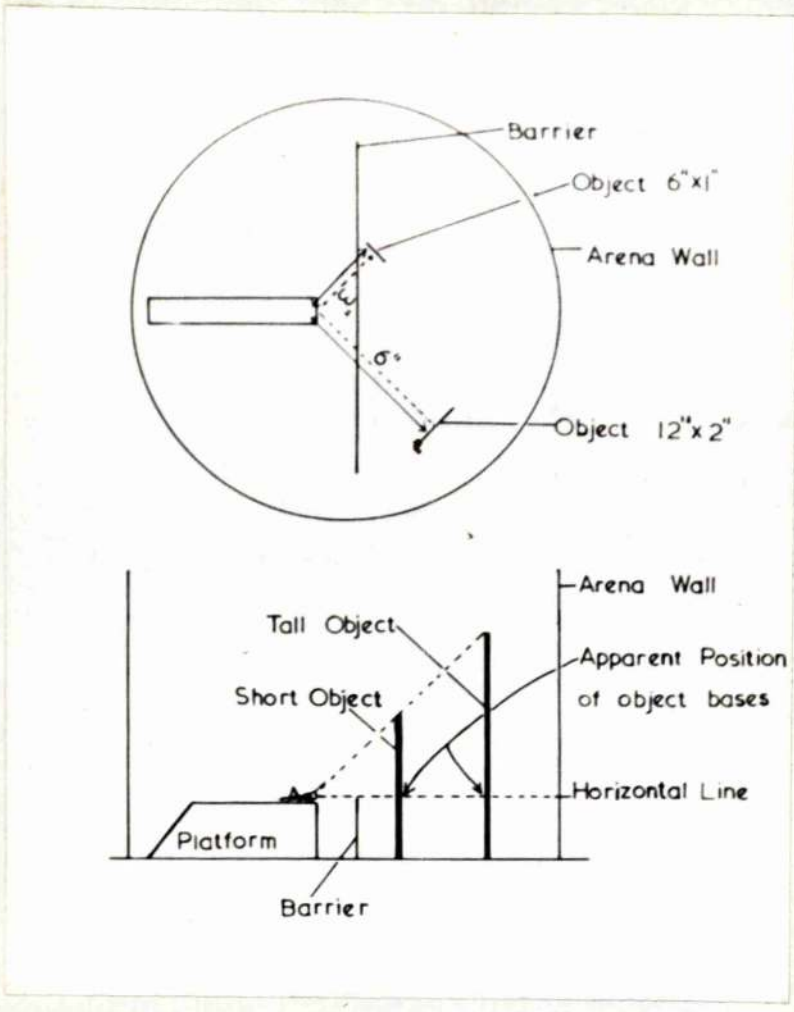


Fig. 9.

Plan and side elevation of the apparatus used to test jumping in response to stationary objects.

of estimating distance. Exner (1891) in discussing distance perception, mentioned, amongst other methods, that for crabs with moveable eyes the rate of apparent movement of the object over the eye could be used as a measure of its distance from the animal. The closer the object, the faster its apparent movement over the eye as the eye is moved from side to side. Now, a locust nymph would achieve exactly the same result by peering and the present investigation was therefore instituted along those lines.

Observation had shown that locust nymphs could often jump on to vertical objects and that such jumps seemed to be accurate with respect both to direction and distance. In all cases (except when the insects are disturbed) jumping is preceded by peering. The ability to jump on certain objects from a distance was therefore studied with respect to the peering which was observed. As a compromise between animals which jump frequently and those with a large body size for ease of observation, fourth instar nymphs were used in all experiments.

Experiments.

These can be divided into two categories, experiments with stationary objects and experiments with moving objects.

Experiment 3 - Peering and Jumping: stationary objects.

In these experiments the insects were presented with two vertical objects and given the choice of jumping on one or the other.

Apparatus and Method. The apparatus used is shown in Fig. 9. It consisted of a narrow platform (6" long, 1" wide, raised 2" off the floor) along

which the insect walked and from the end of which it could jump on to one of the two objects placed in front of it. The whole arrangement was enclosed in a white-walled white-floored arena 2 ft. in diameter and 10" high. The longitudinal axis of the platform was taken as the 0° line as before and corresponding reference lines were drawn on the floor at intervals of 5° from 0° to 90° to right and left of the mid line. By means of these, the objects could be placed at a definite distance and direction from the animal sitting on the end of the platform. The insect's orientation angles were measured by noting the line of the longitudinal body axis relative to the floor line. Except for a few tests with one-eyed animals, the objects were placed at 45° to either side of the 0° line so that for an animal with its body axis on the 0° line the images of the objects appeared on the corresponding parts of each eye. The plain white barrier was just over 2" high and its function was to cut off all vision in directions below the horizontal and thus prevent the animal from judging distance by estimating the relative positions of the object bases.

Procedure. The animals walked along to the end of the platform, stopped, peered, then after a pause changed the body position and peered again. Changes of orientation, always accompanied by peering, might occur several times. Finally the insect would jump on to one of the objects.

The body angle at every orientation was noted and the final choice of object recorded. The actual peering angles were not noted.

The details of the objects, description, size, distance and direction, are given separately for each test. Each animal was tested five times

(five jumps). The results of the object choice in each test are shown in Table 21 .

Test 1. Importance of Distance.

Arrangement. Two plain objects at different distances but subtending the same horizontal and vertical angles from the insect's position.

Objects. Near - black rectangle 6" X 1" at 3 inches distance and 45° to left. Distant - black rectangle 12" X 2" at 6 inches distance and 45° to right.

Results. The results are included in Table 21 . They show that the animals choose the nearer object in almost all cases. The orientations of the animals when peering are given in full in Table 22 .

Test 2. Importance of Size.

Arrangement. Two plain objects at different distances, the farther object subtending a larger vertical angle than the nearer. Nearer object now on the right as compared with being on the left in the first test.

Objects. Near - black rectangle 4" X 1", 3 inches distant, 45° right. Distant - black rectangle 12" X 2" at 6 inches distance, 45° left.

Results. (See Table 21). The animals still chose the nearer object in this situation.

Test 3. Importance of Colour Intensity of Object.

Arrangement. Two plain objects at different distances, but subtending the same horizontal and vertical angles. Objects differing in intensity.

Objects. (a) Near - light grey (YR 10 7/1 Munsell series), 6" X 1" at 3" distance, 45°. Distant - black 12" X 2" at 6" and 45°.

(b) Near - white, 6" X 1", 3", 45°. Distant - black, 12" X 2", 6", 45°.

Results. In both the above cases the animals showed a highly significant choice of the nearer object (see Table 21).

Tests 4 to 7. Importance of Binocular Vision.

In these tests the insects were blinded wholly or partially in one eye. Since locusts are photopositive, they tend to turn to the unblinded side and for this reason in tests 4 and 5 where the objects were on either side, the nearer object was placed on the partially blinded side, so that if there were any slight bias, due to blinding, it would be towards the side of the distant object.

Under a binocular microscope the insects were blinded by application of three coats of black cellulose acetate paint. The animals were examined at the beginning and end of each experiment and in any case where the blinding was defective the animal was rejected. In test 4, the first of the series, the animals were tested three hours after blinding but this did not appear to be a sufficient length of time to allow recovery. When tested after three hours the animals showed little inclination to jump. They walked to the end of the board and then walked all round the end, down the side, often turning several times and moving sideways over the edge. In some cases the animals which jumped somersaulted and missed the object or jumped, banged into the object and dropped. After the blinded animals had been kept overnight or for a whole 24 hours they jumped much more readily. In all other tests after

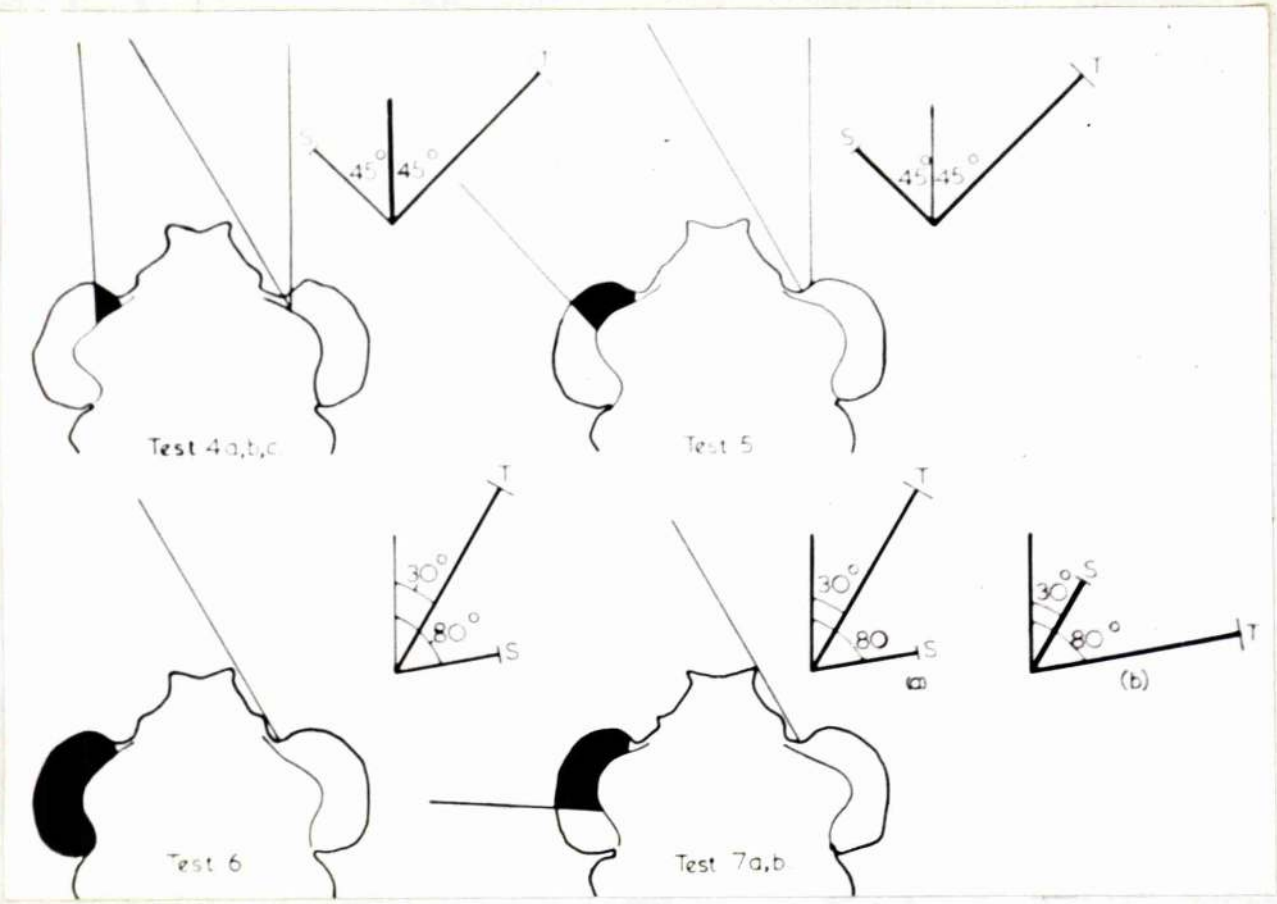


Fig. 10.

Diagram showing the areas of the eye blinded and the positions of the objects in the jumping tests. The head and eyes are seen in horizontal section.

test 4, therefore, the animals were kept for one day before testing.

Details of the blinding performed in each case and the position of the objects are given in Fig. 10 . In test 4 there was no binocular vision directly to the front. In tests 5, 6 and 7 there was no binocular vision in any direction. The extent of blinding was checked by observation of the pseudo-pupil. This is seen apparently on the surface of the compound eye when the eye is viewed under incident illumination. It arises from a group of ommatidia whose optical axes are parallel, or nearly so, to the line of sight. The dark effect is due to total absorption of the incident light by the pigment lying around the retinula cells. The centre of the pseudo-pupil thus represents a line of sight which is directed along the optical axis of the underlying ommatidium (after Burtt and Catton 1954). Binocular vision in the compound eye arises as a result of the intersection of the lines of sight of ommatidia in the two eyes. It is therefore clear that binocular vision exists at any point of the visual field from which the pseudo-pupils of both eyes can be seen simultaneously. The blinded animals were therefore scrutinised under a low power dissecting microscope and the regions of binocular vision which remained after blinding ascertained by the above method.

Test 7. Results. The results of the above test are given in Table 21 and show that even without binocular vision the insects are still capable of choosing and jumping on the nearer of the two objects.

Tests 1 to 7. Discussion. By means of the above tests it has been demonstrated that, when

presented with two plain objects, one nearer than the other, locust nymphs show a consistent choice of the nearer object. (Within the limits set by the test) it has been found that this choice is not based on size or colour intensity, nor is binocular vision necessary. It is quite clear, therefore, that the insects are judging distance on criteria other than these. A close study of the behaviour of the animals prior to jumping provides good evidence to suggest that distance is measured during peering.

Table 22 shows the orientations observed in test 1 and is typical of the readings taken in the other tests. The figures for the other tests are therefore not given. The point to note is that the animals, before jumping, orientate quite accurately towards the chosen object. From this kind of data a further analysis can be made in terms of the sequence of orientation and whether or not they are towards the side of the chosen object. The actual angle of orientation is not used. The results of such an analysis for tests 1 and 2 are given in Table 22a. There is no significant difference between the numbers of first and second positions (~~Table~~ See Col.1 and 2), but there is a highly significant difference between the numbers of the second and third positions (Cols. 2 and 3). In other words the majority of the insects only peer in two positions. Few show a third orientation and fourth orientations are very rare. This is also true of the partially blinded animals in Test 4. In Test 5, (Table 22a) the slightly larger proportion of third positions is probably due to the fact that the animals found it difficult to orientate accurately to

the chosen object in one move. Approximately half the animals peer first in an unbiassed position, midway between the two objects. Table 22b shows that in such cases the second position is almost always facing the chosen object. In other words, the animals apparently "decide" on the basis of the first peering, then turn towards the chosen object, peer in that position, and jump. As will be seen below (Test 8), this is also true when the animals are choosing the further object. (Table 22a, and Table 22b, last line).

The above is thus evidence which, although circumstantial, strongly suggests that the insects are measuring the object distance by the peering movement.

Test 8. If, as mentioned previously (p.55), the insects are estimating the distance and exercising their choice of object on the basis of the transitory stimulation produced by motion of the image over the eye during peering, it should be possible to confuse the animals by increasing this stimulation. This can be done either by increasing the number of contours moving over the eye or by increasing the speed of apparent movement. In the test described below the first method was used.

Arrangement and objects.

(a) Near - plain black rectangle 6" X 1" at 3" distance and 45°. Distant - black rectangle 12" X 2" subdivided by two vertical light stripes each 0.4" wide and 12" long (~~Fig.~~) at 6" distance and 45°.

(b) This was the same as (a) except that here the further object was subdivided with horizontal white stripes.

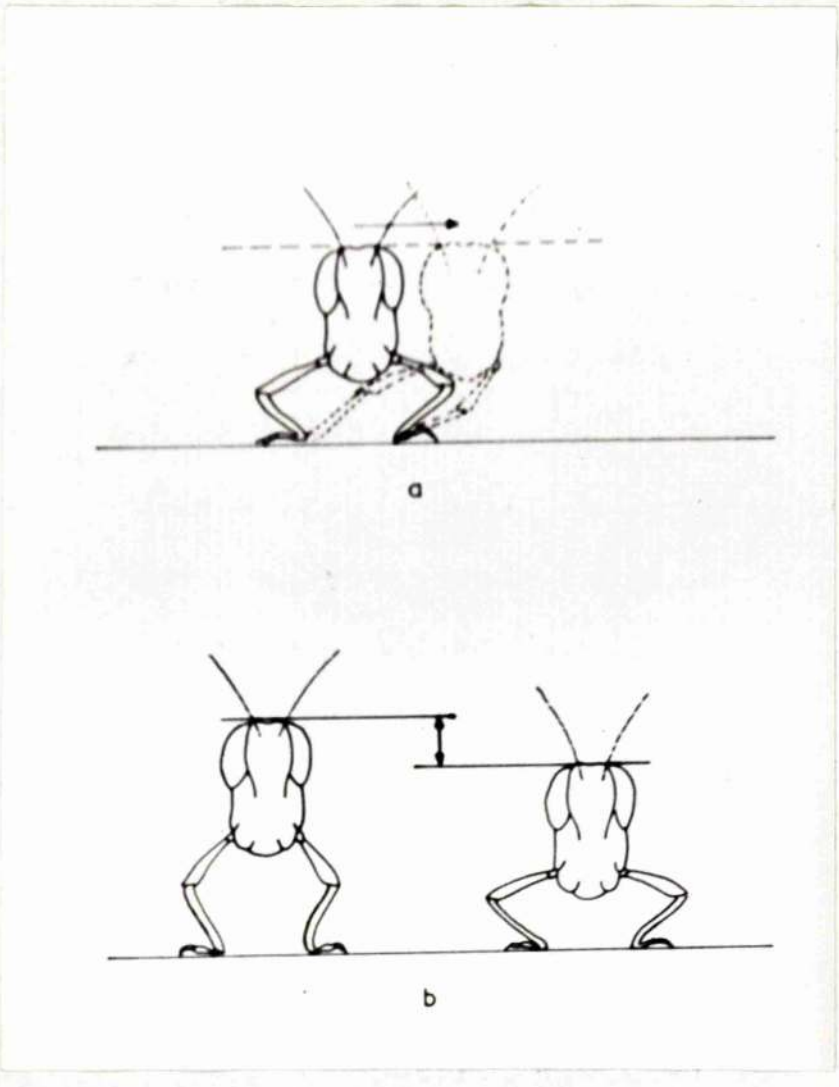
(c) Both 12" X 2" at 6" and 45°. One object subdivided vertically as in (a) and one subdivided horizontally as in (b). It was so arranged that there was the same area of black and white on each object and that the length of the vertical black/white contour on the first equalled the length of the horizontal black/white contour on the second. One set of results was taken with the vertical object on the right and the horizontal on the left and a second taken with the positions reversed.

(d) Control experiment. This was the original situation with two plain black objects. Near - 6" X 1", 3" distance, 45°. Distant - 12" X 2", 6", 45°.

Test 8. Results. The results of the above tests are given in Table 23.

Test 8. Discussion. The results of this test show that subdivision of the more distant object either by vertical or horizontal white stripes renders that object slightly more attractive than the nearer one and produces a highly significant change of bias from that found in the control where both objects are plain ($p<.01$). The vertical subdivisions are more effective than the horizontal ones, for objects of the same size and at the same distance ($p<.01$), a result in agreement with the hypothesis that during peering the animal is measuring the amount of transitory stimulation produced by image movement over the eye. When an animal is moving horizontally, as in peering, the vertical stripes would be expected to produce the greater stimulation.

The attractiveness of the object with the horizontal white stripes



Fig, 11.

Diagram illustrating how a vertical component of head movement is produced.

As shown in a there is no vertical movement of the head during the horizontal peering movement. However, the insect will frequently peer with the head high off the ground(b1) and then again with the head lower to the ground(b 2).

as compared with the plain object (test 8b) remains to be explained. Horizontal contours will provide transitory stimulation only when there is a vertical movement of the insect's eye. Is such a movement present? Close observation shows that there is no noticeable vertical component of movement when the head is being traversed horizontally during peering. However, between successive peerings there is often a considerable raising or lowering of the head due to a stretching or bending of the front legs (see fig. 11). Also, when the insect walks forward or back for even a small distance the horizontal contours must move vertically over the eye. It is possible, then, that there is sufficient vertical head movement to give rise to transitory stimulation from horizontal contours. This would explain why the horizontally striped object was preferred to the plain one.

Such movements of the horizontal contours, produced as described above, would however be small when compared with the much larger displacement of the vertical contours which occurs during peering or walking. Hence vertical contours will produce more stimulation than horizontal ones and vertically striped will be preferred to those with horizontal stripes (test 8c).

It should be noted that even here where the insects are choosing the farther object the majority still only peer in two positions (Table last line), and that where the first position is unbiased, the second position is almost always facing the chosen object (Table 22b last line).

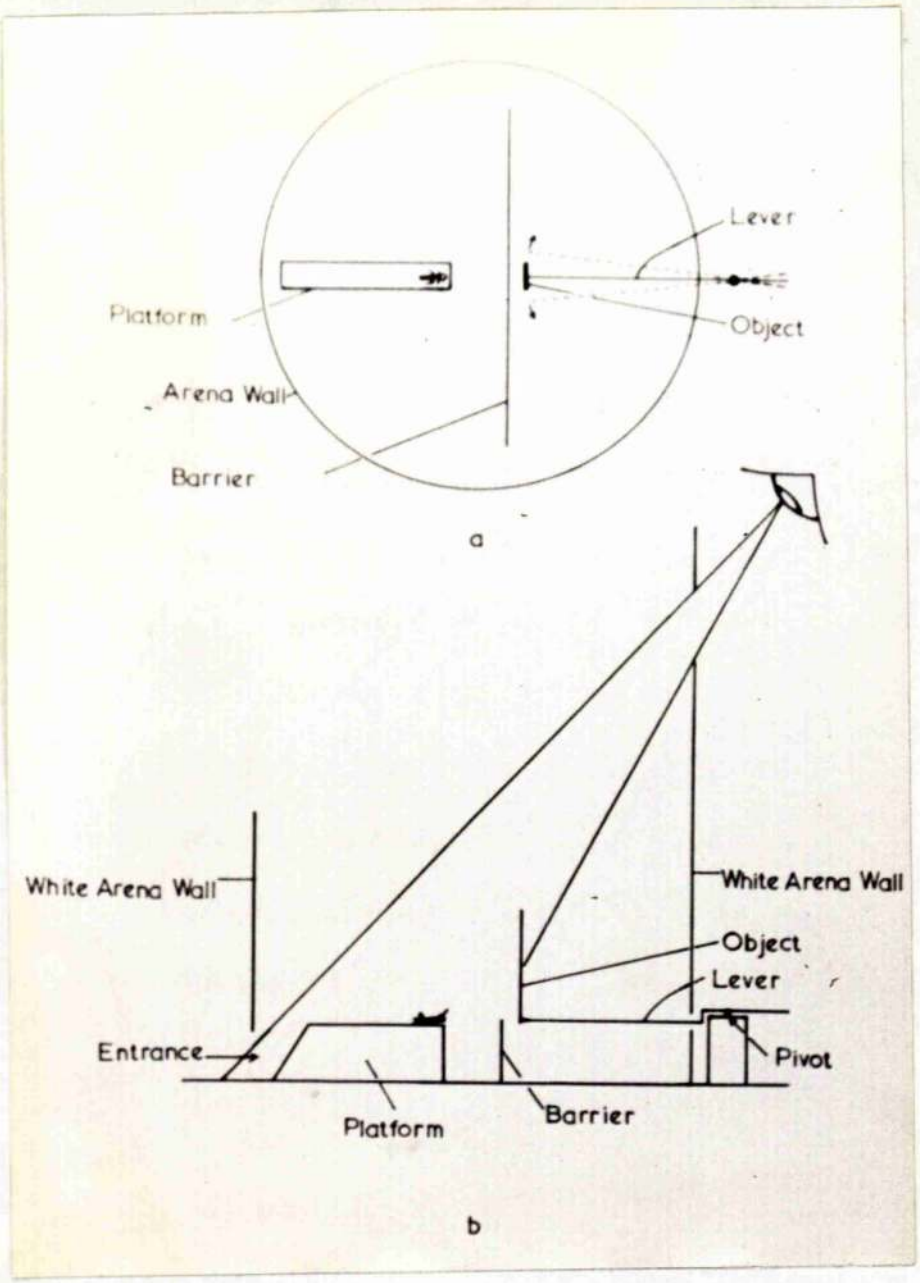


Fig. 12.

a - Plan view, b - side elevation of apparatus used in the jumping experiments with a moving object. For description see text.

Experiment 4. Peering and Jumping: moving object.

In this experiment the insects were presented with an object which was moved slightly whenever they peered at it. By this means it was hoped to confuse the insects by increasing or decreasing the apparent movement of the object relative to the animal.

Apparatus. The apparatus is shown in Fig.12 . The object was a black rectangle, 4" tall X 1" broad, at a distance of 3.5". There were two experimental conditions, "moving against" and "moving with". In the former, every time the locusts swayed to one side in peering, the object was moved slightly in the opposite direction. In the latter the object was moved in the same direction as the animal. Controls were run with the objects stationary. Note was taken of whether the animal jumped on to the object, overshot it, or jumped short of it.

Results. These are given in Table 24 .

Discussion. It is clear from the results of the above experiment that when the object is stationary, the insects seldom miss it, whereas when it is moved in the opposite direction to the animal's peering motion, they misjudge the distance and in almost all cases they jump short. They never overshoot. When the object is moved "with" the insect, the insect can manage to jump on to it in most cases; it may occasionally jump short or overshoot.

It is to be expected that when the object is moved "against" the insect's motion the apparent movement of it as perceived by the insect

is much greater than it would be for a stationary object at that distance and is equivalent to the apparent movement if a stationary object at a very close distance to the insect. This is apparently how the insects interpret the information received and explains why they jump short. This is borne out further by the fact that the insects were observed to beat the antennae vigorously and to stretch out the first pair of legs and "paw" in the air as if attempting to climb on an object extremely close to them.

When the object is moved "with" the insect the reverse occurs and the object appears to be much further away than it really is. This does not, however, prevent the animals from jumping on it, since, if their direction is correct, they will encounter the object during their trajectory. Hence the number of hits in this case is significantly greater than the number of misses. If the direction is not accurate, they may overshoot.

It could be argued that a moving object would also upset an estimation of distance by binocular vision since the insect would find it difficult to fix the object and that therefore the present evidence is no proof that apparent movement is being used. However, against this it can be stated that (a) the insect cannot fix a point accurately if it moves its head from side to side as it does in peering and (b) that a movement against the animal causes it to jump short consistently, i.e., in one particular way as predicted by the estimation of movement hypothesis. The animal does not jump short and overshoot as might be expected if distance estimation were merely upset generally. Furthermore, it has been shown

that binocular vision is not essential (see p.60).

From this experiment therefore there is very strong evidence to support the hypothesis that peering is a means of distance estimation based on the measurement of apparent object movement as already detailed above.

Peering - A General Discussion.

Peering in locusts has been shown to be a visual response influenced by the presence and position of objects in the visual field. There is very strong evidence for concluding that it is a method of estimating distance, in which case it is, of course, to be expected that it would be a prelude to orientation, i.e. in this case to the taking up of a particular direction of the horizontal axis of the body with respect to the surroundings. This has in fact been demonstrated both in the case of a locust nymph which is walking and in the case of one which is preparing to jump.

Although peering is influenced by the position of objects in the visual field there is no reason to suppose that it is a method of estimating the direction of such objects. It would seem that the compound eye by virtue of its large visual field and numerous elements is an ideal direction analyser even when stationary* and that hence, the movement of the head during peering is not necessary to any estimation of direction.

Many of the peering angles are small and unaffected by the position of objects and it is likely that these are preliminary scanning angles (see p.51). It was observed that they did, in fact, precede the larger

* See later p. 69 line 15 .

biassed peering angles. In other words, locusts peer either when looking at something, i.e., measuring the distance of a particular object, or when looking for something, i.e., when scanning the surroundings. On this basis the observation made by Chapman (1955) that locusts peer in a uniform visual field is understandable. From observation of highly excited animals the impression was gained that peering in such cases might be a displacement activity (Tinbergen, 1951). This explanation may remove Chapman's second objection that peering sometimes occurs when the head of a hopper is touching some obstruction immediately in front of it.

It seems to be generally accepted (Wigglesworth, 1953, Roeder, 1953) that in insects with highly developed compound eyes, distance estimation is accomplished by means of binocular vision. This is based on the work of Baldus (1926) and Friederichs (1931). It is perhaps significant that both these authors worked with predatory insects, Aeschna nymphs and Cicindelid adults respectively. In both cases extremely short distances are involved, in the first case the length of the labial mask and in the second the length of the mandibles. While it is clear from these works that binocular vision does give accurate distance estimation over these short distances, a little consideration will show that the accuracy will fall off with distance. At large distances therefore, such as those covered by a locust when jumping (e.g. 18"), it is possible that the binocular method is no more accurate, and perhaps even less accurate than distance estimation based on apparent movement. No experiments in the literature give any idea of the accuracy of binocular vision at large

distances.

At this point the theory of the binocular method of distance estimation must receive comment. This theory was first put forward by Exner (1891) and it was based on the assumption that in the apposition type of eye the ommatidia were so separated as to receive light from a very small part of the visual field. This part was that area subtended by the solid angle of the ommatidium which in turn equalled the inter-ommatidial angle. Burtt and Catton (1954) have recently shown that this is not true; that each ommatidium receives light from a much wider area than that subtended by the inter-ommatidial angle and that therefore the visual fields of adjacent ommatidia overlap. This fact is referred to more fully in the appendix to this thesis. Suffice it to say here, however, that although these findings might be thought to invalidate the theory of binocular distance estimation, consideration shows that they do not necessarily affect the principle of the theory. (See appendix I, p.135).

The existence of a binocular method of judging distance (at least short distances) is therefore not called into question, but it is doubtful whether such a system operates at longer distances.

It is true that the present experiments on peering give no measurement of the limit of accuracy of distance estimation achieved by this apparent movement method. Nevertheless it has been shown that the compound eye is extremely sensitive to very small movements (Burtt and Catton, 1954 and 1956).* It is therefore possible that even when objects are at relatively

* 100% response to movement of .33°. Five out of ten responses to movement of .1°.

long distances and their image movement over the eye correspondingly small the insect can still measure this accurately.

It is not intended to convey the impression that peering is the only method of distance estimation used by locusts, simply that it is one of the methods involved and possibly that one in use at larger distances. There is a fairly large binocular field (30° to either side (Whittington 1951)) and binocular vision may be used, particularly at shorter distances.

Again, it is not suggested that distance judging is the only function of peering. Autrum has expressed the opinion that without movement insects can see nothing (personal oral communication). If this is so, peering may have a much more general function in addition to distance estimation. It is possible that the image movements produced by peering allow the insects to form a much more accurate impression of their optical surroundings - the shape of objects and even their positions. (See general discussion and appendix).

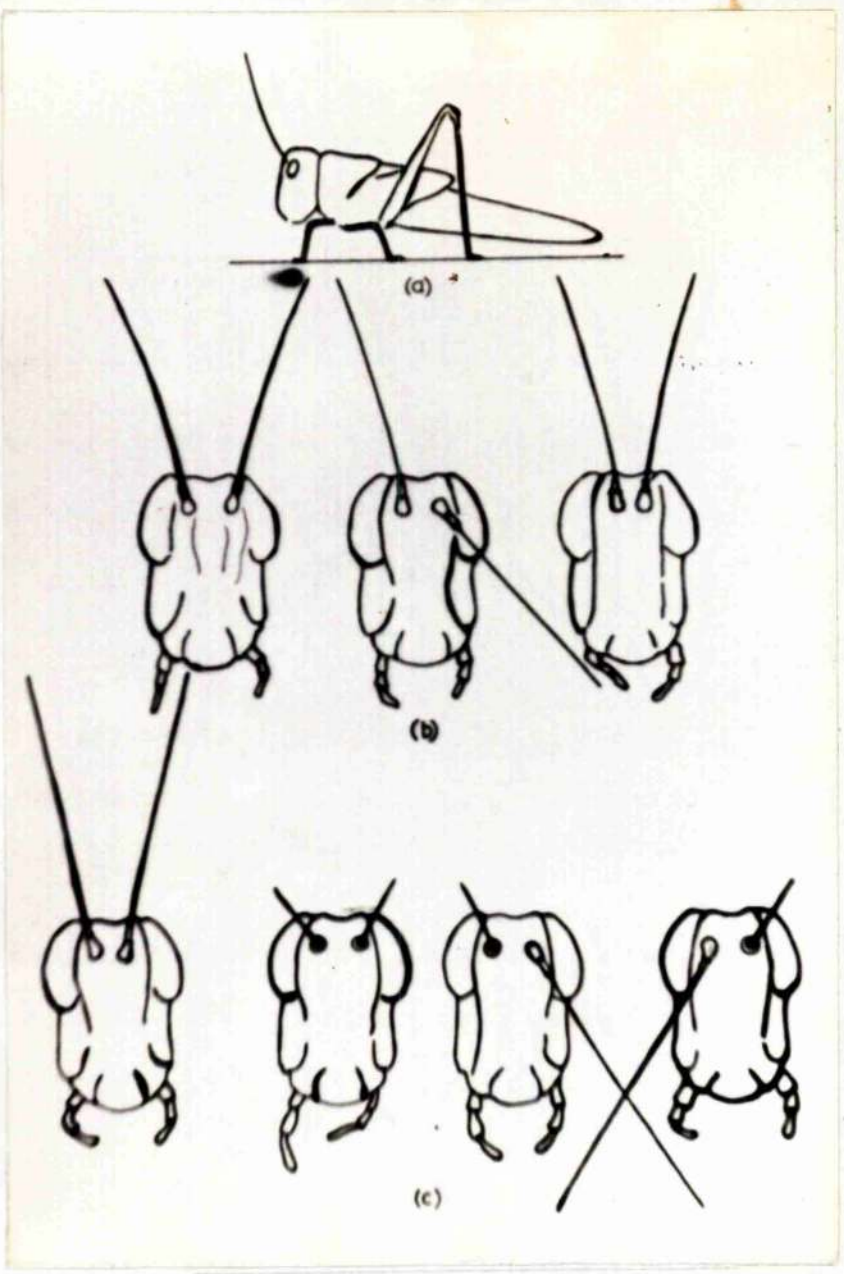


Fig. 13.

Diagram showing the positions and movements of the antennae referred to in the text.

a - antennae in the erect position while the insect is walking.

b - flicking of the left antenna.

c - beating of the antennae.

The time sequences read from left to right in each case.

ANTENNA WAVING.

Introduction.

As already mentioned, during the course of the form perception experiments, it was observed that when the locust nymphs approached an object the antennae were waved. It was also observed that when the animals were passing close to an object there was again an antennal movement. It has been shown in a few cases that antenna waving in Arthropods is sometimes released by visual stimuli (Bröker, 1935; Schiller, 1937; Wolf and Zerrahn-Wolf, 1935; de Wilde, 1940). It was thought that the antenna waving observed in locusts was a response of this type. From observation one gained the impression that the response only occurred when the animals were fairly close to the objects and it was therefore thought that the antenna waving reflected an ability on the part of the insects to judge their distance from these objects. There might therefore be a means of judging distance other than by peering and a detailed investigation was therefore made of the exact stimuli releasing the response.

Preliminary observation had shown that there were at least two different kinds of antenna movement, flicking and beating.

Flicking - This is a movement of a single antenna. When the insect is walking, the antennae are held erect, pointing slightly forward at a small angle to the vertical (Fig. 13b). In flicking one antenna is briefly lowered a short distance (not usually to the floor) and then raised. The insects may flick several times. In conjunction with the flicking there

may be pointing of the antenna in which the antenna is moved from the forward position and pointed to the object.

Beating - This is a movement of both antennae, which occurs when the antennae are in the forward position. The antennae are lowered from the erect position to point horizontally forward and then they move rapidly up and down. The beats are alternate, one antenna going up while the other is coming down. (Fig.13c). In beating the movement is faster than in flicking.

Flicking occurred when a hopper approached an object obliquely or walked past an object lying to the side. Flicking was seen up to 4 or 5 inches away from an object. Beating occurred when the animal was much closer and head-on to an object.

When a nymph approached an object obliquely flicking would occur first and then as the distance became smaller and the animal more head-on to the object, beating commenced.

The first experiment was designed to allow more detailed observation of the antenna movements as the insects approached an object.

Experiments.

Experiment 1.

Apparatus. The animals were tested in the form perception arena with four black stripes (8" tall by 1" broad) equally spaced on the wall. With the mid-point of the stripe base as the centre, very faint concentric semi-circles were drawn on the floor, one inch apart, the outermost 5" from the stripe. By this means the insect's distance from the stripe could be

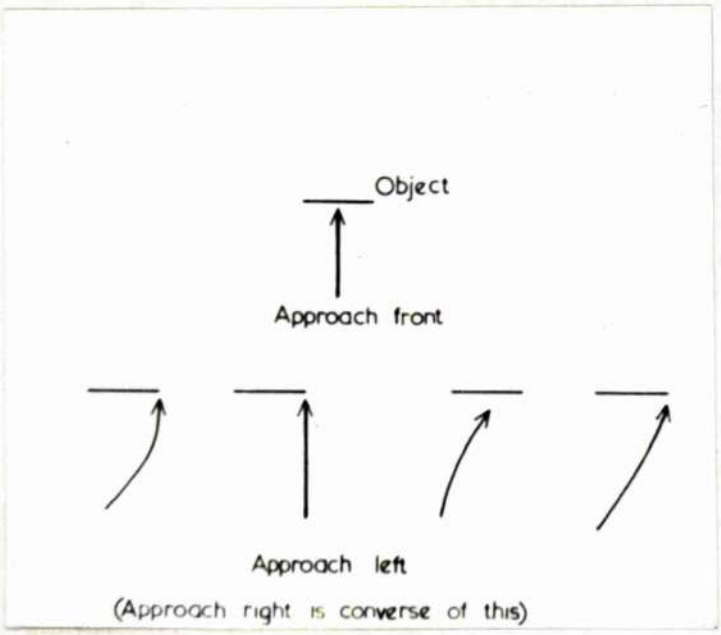


Fig. 14.

Diagram illustrating the meaning of the terms "approach front" and "approach left". See text p. 72.

noted. It seemed reasonably clear that these faint lines were not responsible for releasing the antenna flicking. It is true that marks on the floor are investigated with the antennae but in such cases the antennae are pointed down to touch the marks. This was not seen in the present experiment. In many cases the antennae were clearly being pointed at the vertical edge of the object. The same argument applies to the subsequent experiment in which there were lines marked on the runway. In addition, in both experiments the insects did not flick the antennae as they crossed each and every line as might be expected if the antenna movement were a response to the line.

Procedure. The insects were placed singly in the arena and observed. When they approached the stripe the direction of approach was noted and the antenna which was first moved was noted, along with the distance at which this occurred.

Animals. As in all the antenna-waving experiments fifth instar nymphs of the normal gregarious phase were used.

Results. The results are presented in Table 25. The beating which followed the flicking took place so close to the object (approximately one inch or less) that in this experiment it was impossible to note the exact distance at which it occurred. Beating is thus omitted from the table. The approaches were classified as shown in Fig.14. An animal made a "left approach" if it approached on such a course that the left side of the body was nearest the object.

An animal was accounted to have responded positively if the antenna

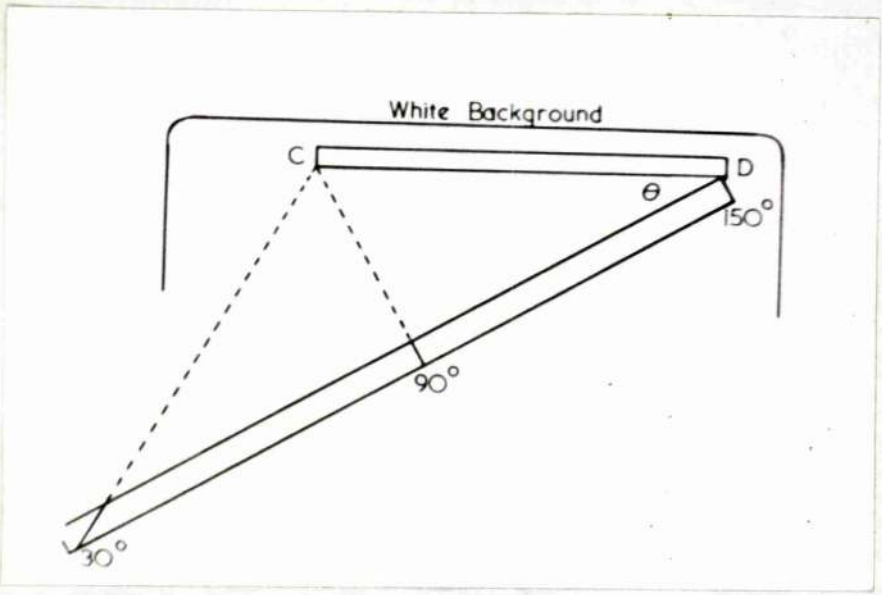


Fig. 15.

Plan view of apparatus for studying flicking of the left antenna as ~~xx~~ a nymph approached an object obliquely.
AB narrow runway 1" broad.
CD black rectangle 4" tall,6" broad.
θ angle of approach.
The numbers on the runway indicate the bearing of the edge C from the particular points(in degrees).

first waved was the one on the side nearest to the object during the approach. Of the thirty three runs made with six different animals, twenty seven were positive and six negative, which demonstrated quite markedly that it was the antenna on the side nearest to the object which was first flicked. The measurements in the table give some indication of the order of the distance at which this occurred; however, since the angles of approach varied considerably, nothing further can be deduced from these distances.

Flicking.

In the following experiment more detailed observation was made of the antenna flicking which occurred under controlled directions of approach to an object.

Experiment 2.

Apparatus. This is shown in Fig. 15. AB was a long narrow runway placed obliquely to a vertical black rectangle 4" tall and 6" broad (CD) so that the end of the runway abutted on to the right hand edge of the rectangle The animals were allowed to climb on to the runway at A and walk along it in the direction of the right hand edge of the rectangle at D. In so doing they passed the left hand edge of the object (C).

Faint lines drawn on the runway at several points indicated the bearing of C from those points in degrees. These marks were at intervals of 10 degrees running from 30° at A to 150° at D.

As the animals walked along the runway note was taken of the point at which the left antenna was first moved. The right antenna showed no movement but the left antenna was flicked.

Animals. These were 5th instar nymphs of the gregarious phase. They were tested singly, 25 runs being made with 5 animals.

The experiment was repeated with an angle of approach = 60°.

Results. These are given in table 26 and show that the antenna flicking began when the object edge C bore a definite relationship to the animal's position, i.e. between 60-70 degrees. The angles varied from 40°- 90° with an average of approximately 62-63 degrees, Since, however, the accura for both approach angles of 30° and 60° of measurement was only to within 10 degrees the actual figures should not be stressed.

In many cases it was noticed that when the animal had walked past the edge C i.e. bearings of over 90 degrees, the left antenna was moved round posteriorly to point still in the direction of the object edge.

Conclusion. The results obtained and the observations reported above strongly suggest that the antenna flicking was a response to the vertical edge of the object. In the two cases (30 and 60 degree pproach) the flicking occurred at different distances from the object but at approximately the same bearing to the vertical edge.

Experiment 3.

This test provided further evidence in support of the idea that the antenna flicking was a response to the vertical edge.

Apparatus. The broad rectangle of the previous experiment was replaced by a narrow rectangle 4" tall by 1" broad placed so as to occupy the same position as the left hand edge (C) of the original rectangle.

Animals. Fifth instars of the gregarious phase. 5 animals were

tested each 5 times.

Results. In every case the antenna flicking was observed as before. The average bearing was 56 degrees (see Table 26).

Since there was no distant edge to attract them to the far end of the runway the insects tended to turn towards the object as they drew level with it. For this reason the angles recorded cannot be regarded as accurate measurements of the angles between the object and the animal's body.

Antenna Flicking - Discussion.

From the results and observations reported above it is concluded that antenna flicking is a response to the edge of an object (in this case the vertical edge) appearing on the lateral part of the eye. It is not merely a sign of general excitation caused by the proximity of the object for there is a strict correlation between the antenna waved and the side on which the object is situated. It is almost certainly a visual response because of the accuracy in the pointing of the antenna at the vertical edge of the object.* It is not, in the present case at least, a response to the horizontal edge of the object nor is it released by the gradual approach to the surface of an object since, when the object is reduced to a narrow vertical stripe, the response still occurs at the normal position (expt. 3).

The importance of the response is discussed further in the discussion (p.89).

* Further observation confirms this. Thus, the animal blinded in one eye show no flick of the antenna when passing an object on the blinded side.

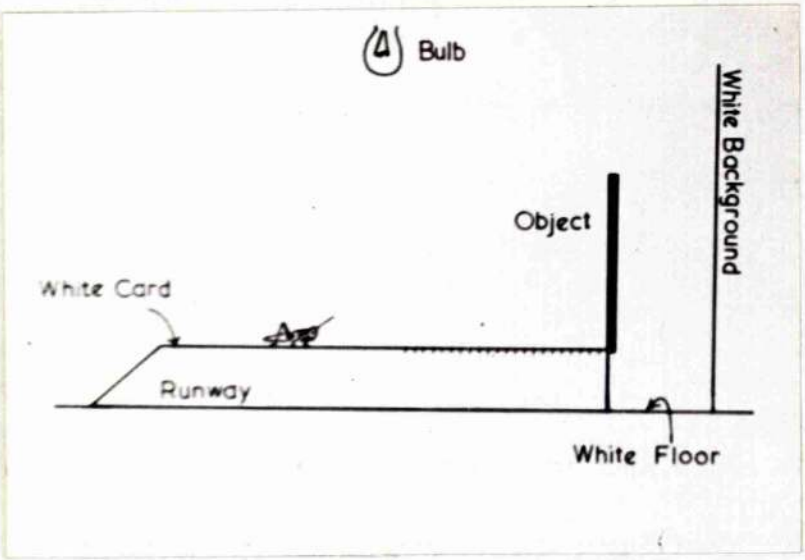


Fig. 16.

Side view of apparatus for studying the antenna beating which occurred when a locust nymph approached a vertical object.

Beating.

In order to study more accurately the beating which occurred when a hopper was close to an object, an apparatus was arranged by which the insects were made to approach head-on to an object and which allowed the antenna movements to be closely observed. Fig.16 shows a diagram of the arrangement. The animals were observed from the side and the distance noted at which beating first occurred. The apparatus was surrounded on three sides by a white background as shown and this ensured, that first, the objects were seen by the animal against a white background, and second the antenna movements could be clearly seen when the animal was viewed from the side against a white background. Lighting was from a 60 watt bulb 18" directly overhead. The observer sat with his eyes on a level with the animal. Experiments were performed in which the size, nature and position of the object was varied.

Experiment 4. Black rectangles of different sizes.

In this short series the objects were black rectangles of different dimensions. The aim was to test the effect of object size on the distance at which beating occurred.

Apparatus. The objects were as follows:-

Objects	Breadth	Height
a	1"	4"
b	1"	12"
c	12"	4"

A comparison of the results for a and b tested the importance of height and comparison of a and c tested the importance of breadth.

Results. The results are set out in Table 27. Analysis of the variance and comparison of the means showed that neither breadth nor height had any significant effect on the distance at which beating first commenced. There was a large degree of variation but the mean distances are in all cases quite short (.65"; ;76"; .82"). The animals walked along the runway with the antennae erect until, when close to the object, beating occurred. The animals continued to approach the object, touched it with the antennae and climbed up it, in many cases climbing diagonally out to one of the vertical edges. The complete beating was not observed in every case. In cases where the distances were short the antennae were brought forward but almost immediately came into contact with the object.

From this experiment these facts were elicited:-

1. Beating occurred at short distances (within one inch).
2. All animals were found to show it.
3. The distance of beating was independent of the object size.

Discussion. It was clear then, that by some unknown means, the animals could detect that they were close to an object. The problem was then to discover what "cues" they were using for this. It did not seem likely that they were estimating distance by binocular vision for they were forced to approach the centres of the objects and could not "fix" the vertical edge binocularly, and since the objects were perfectly plain (at least to the human eye) it seemed unlikely that they could "fix" any detail within

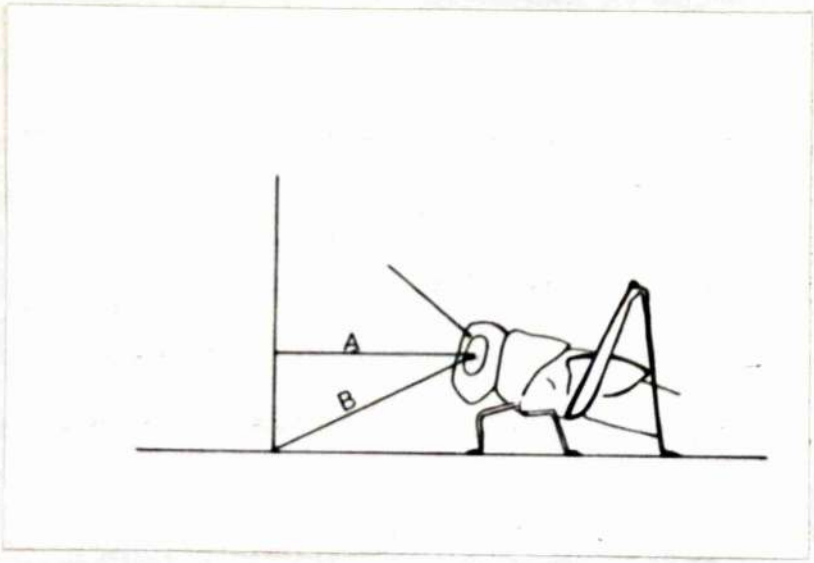


Fig. 17.

Diagram illustrating a possible method for judging the distance of vertical objects.
A - line of sight of horizontally directed ommatidia.
B - line of sight of ommatidia seeing the base line of the vertical object.
The angle between A and B gives a measure of the distance of the object from the insect.

the object itself. Hundertmark (1937b) showed that caterpillars estimated distance on the basis of the vertical angle subtended by the object. This could not be the mechanism in the present case for the distances at which beating occurred were independent of the object size.

It was extremely difficult to visualise what the insects were reacting to. When very close to the object, the visual situation would be closely analogous to that of a man standing fairly close to a very large blank wall on which no details were visible and looking straight in front of him (~~see Fig. ___~~). Personal experience and tests with one other subject showed that in such a situation it was extremely difficult to form any estimation of the observer's distance from the wall. If the head and eyes were lowered so that the line could be seen where the base of the wall joined the floor, it was possible by noting the amount of head and eye movement to obtain a good estimation of the distance from the wall. The same might apply to the insects (Fig.17). Here of course there would be no need to move the head, the more ventrally directed ommatidia would see the base line of the object. The more ventral the ommatidia seeing this line, the closer the object. The hypothesis was tested in the next two experiments where the position of the base line was changed.

Experiment 5. Base line raised.

The object at the end of the runway (4" black square) was raised so that its base was 0.5" off the top of the runway. In this position the base line was slightly above the horizontally directed ommatidia of the eye.

If the insects lowered both antennae from the erect position before hitting the object, they were accounted positive; if not, negative. The animals used were 5th instar nymphs. Ten animals were tested, each five times, and the experiment was then repeated with a further group of seven animals. A control was run with the object lowered on to the runway in the normal position.

Results. The results are given in Table 28.

It is immediately clear that the raising of the base line decreased the number of positive responses to a marked degree. In the normal situation, with the object standing on the floor, very few animals failed to show the antenna movement as they approached. On the other hand, with the object in the air, the majority of the animals failed to respond, they walked along with antennae erect and in some cases whenever they hit the object, they stopped. Sometimes they "ducked" down when the antennae hit the object and walked on underneath it. In several cases the animal, when approaching the object, straightened the front legs so as to raise the head and thorax above the normal position.

Experiment 6. Base line lowered.

The object (4" black square) sat on the end of the runway, but the runway, instead of being completely white, was painted black from the foot of the object to a distance 3" away from it. It was hoped thus to present the animal with a false base line 3" away from the object, the real base line, where the black objects met the black floor, being invisible. The animals were only accounted to have responded positively if the antennae

were moved before the head reached the artificial base line. Animals which started beating when the head was over the base line or beyond it were scored as negative.

Results. The results are set out in Table29 , and the average distances for the positive responses are given.

The majority of the animals responded positively, showing that the false base line could release antenna beating. Most of the animals continued to beat all the way from the false base line to the object itself. Several v riations in behaviour were observed. Thus a few animals paused before the base line and in one case the animal then moved cautiously forward with the antennae extended horizontally as if "expecting" to hit a vertical object. In a few other cases the animals started beating before the baseline, then paused about 1" past it and then approached the object with antennae beating. In most cases the antennae were held horizontally while beating but in a few cases they were pointed down at the base line. It seemed quite clear, however, in all the positive cases, that the false base line was the stimulus causing the animals to beat at such a long distance from the real vertical object.

Experiment 7.

If the base line were the only important stimulus for releasing the antenna beating there was every reason to suppose that animals walking on a black surface and confronted with a white object would show the response for the black/white base line would still be distinct.

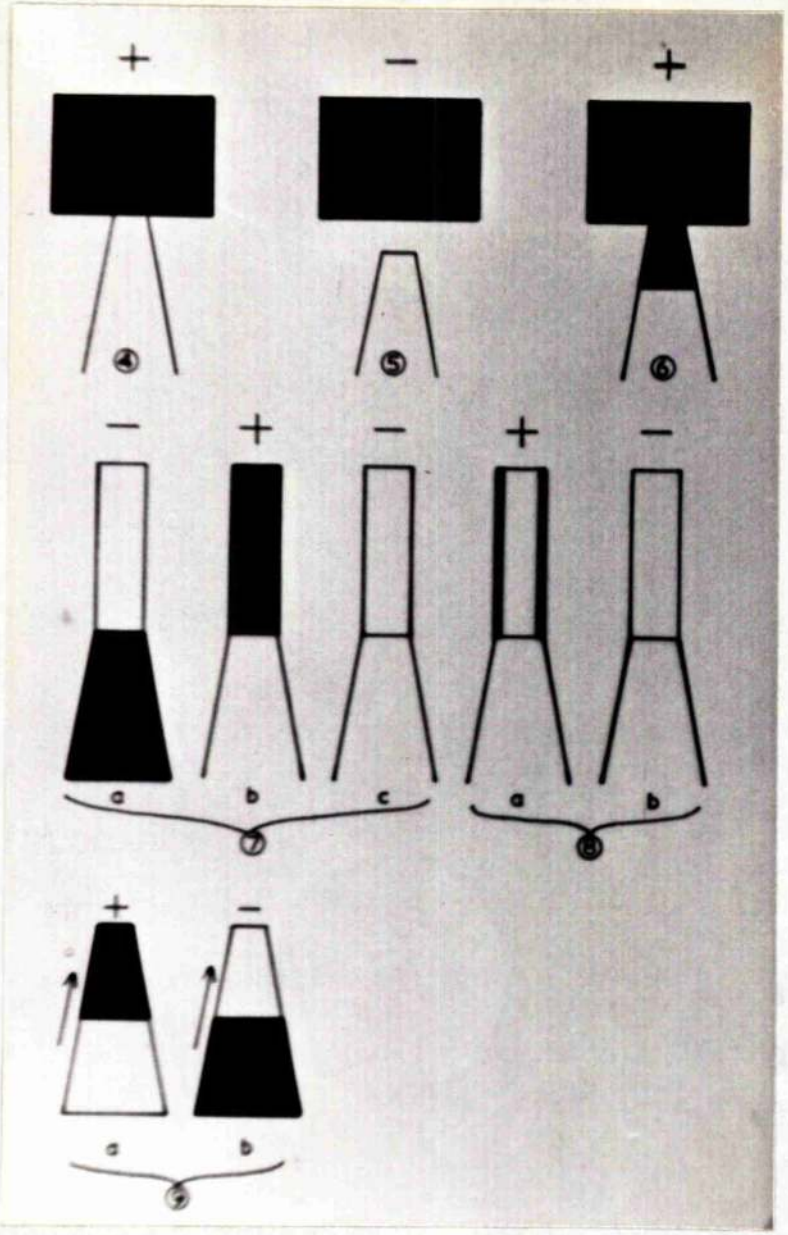


Fig. 18.

Résumé of experiments 4 - 9 for studying antenna beating.
Diagramatic views of the visual situations in these expts.
as perhaps appearing to an insect walking along the runway.
The oblique lines represent the runway in perspective.
Vertical lines represent the edges of vertical objects(there being no vertical object in expt. 9).
+ indicates that in this situation antenna movements were seen.
− indicates " " " " no antenna movements were seen.
(Compare the side)view of the arrangement as shown in Fig.16).

Accordingly this was done. The experimental runs were made with a black runway and a white rectangle 4" tall by 1" broad. The controls were of two kinds (1) white object 4" by 1" broad on a white runway and (2) black object 4" by 1" on a white runway (see Fig. 18).

Results. The results are presented in Table 30.

Although the number of animals tested was small, an extremely curious fact was at once obvious. Animals on a black floor confronted with a white object showed no more response than to a white object on a white floor, in both cases walking straight into the object with the antennae still erect. The same animals showed perfectly normal responses to the black object on a white floor. The lack of response in the case of white object/white floor was understandable since the base line was not obvious, but there was no reason to suppose that the base line where the white object joined the black floor was not visible to the animals. One difference which existed between the situations "black object/white floor" and "white object/black floor" was that, since the arrangement was set up against a white background, the white object was not visible to the animal, only its base line. Fig.18 shows the optical situations diagrammatically. Up till now attention had been focused on the importance of the base line alone, but it was extremely possible that the object itself played some role in releasing the antenna beating. The very first experiments had dismissed the actual size of the object as being of any significance but the mere fact that a vertical object was visible to the animal might be important. This was tested in the next

experiment.

Experiment 8.

Using a white background and a white runway the animals were presented first with a plain white object (4" tall and 1" broad) and then with the same object with the addition of a narrow black stripe (1/16" wide) on each vertical edge.

Results. These are given in Table 31. For the most part the animals walked straight into the plain object without even moving the antennae from the "erect" position. No beating was ever observed, the only movement was a lowering of both antennae to explore the faint base line. When the vertical edges of the object were picked out in black beating occurred in a great many cases, dipping of the antennae was also observed in some cases combined with beating, the antennae pointing downwards and moving alternately. Quite clearly the vertical edges played an important part in releasing antenna beating. The proportions 14:36 and 40:10 (Table 31) were compared by the X^2 test and were found to differ significantly ($P < .01$).

The importance of the base line had now to be re-examined independently of any vertical object (all previous experiments had included vertical objects).

Experiment 9.

In this experiment the animals were made to walk along a long runway of which half the length was white and half black. This was placed inside a white arena (diameter 2 ft.) on a white floor. The animals

were placed on one end and as they walked along to the other end their behaviour was noted. They were tested both walking from white to black and in the opposite direction. Animals showing movements of both antennae at the black/white boundary were scored positive.

Results. These are given in Table 32.

From them it is at once clear that far more responses were obtained when the animals crossed from the white to the black than when traversing the opposite path. The antenna movements at the boundary consisted in the antennae being brought forward and pointed down at the boundary. This was clearly quite a separate response from the normal beating and the word "dipping" was used to describe it. In many cases, the insects, when walking from white to black, paused briefly about one inch before the boundary and then moved forward again with the antennae dipping to touch the boundary or close to it.

The question which had now to be answered was why there should be more responses when the animals walked from white to black than when walking from black to white. There were two possibilities, either (1) the black part of the board was more effective in releasing the response because it contrasted with the white background (walls and floor) or (2) the antenna movements were released by the darkening of the visual field which occurred as the animal approached the black part of the runway, but not by the brightening which occurred when it crossed in the opposite direction. The final experiment arranged to test this was so designed as to obviate the first possibility and to test the second alone.

Experiment 10.

Apparatus. This was simply a white arena 2 ft. in diameter with half the floor made of black card and half of white. The sections were laid accurately edge to edge so that the boundary was completely smooth. An animal was placed in the centre of one side of the arena and a tall black object (8" X 2") placed diametrically opposite on the other wall. To this the animal was attracted and hence was induced to cross the black/white boundary at approximately right angles. Since the object was 12" from the boundary it is highly unlikely that it contributed in any way to the antenna movements seen at the boundary. (See p. 77 beating occurs within 1" of vertical object). Without the object the animals seemed to wander about at random and if they crossed the boundary they often did so at a very oblique angle. When the animal had walked from one side to the other the object was placed on the opposite side and the animal observed as it walked back over the boundary in the opposite direction. Animals were only accounted positive if they showed a movement of both antennae. This took the form either of the normal beating or of dipping and occurred when the head was about ½" from the boundary. The distances were not recorded. Animals which showed only a flick of the antennae or no movement at all were considered negative.

Results. The results are given in Table 33.

Conclusion. In contrast to the behaviour in the experiment with the black and white runway, the insects gave a significant number of positive

responses when walking from black to white. There was however a significant difference between the proportion of positive to negative responses when the insects were walking from white to black and when they were walking in the opposite direction. There is thus some evidence to suggest that a darkening of the anterior part of the visual field is more effective in releasing the response than is a brightening of this part.

Experiment 11.

This was a further check on whether or not binocular vision was important for releasing antenna beating. It was not possible to experiment with one-eyed animals (thus destroying the binocular vision) for painting the eye of one side greatly affected the movement of the antenna of that side and in rare cases stopped it altcgether, thus making it impossible to observe beating.

Apparatus. This was a black arena with a white floor so that the animals were confronted by a vertical object without a vertical edge and with only a base line. The walls were perfectly plain (to the human eye). In these conditions it should be impossible for the insects to use binocular vision for a horizontal base line cannot be fixed binocularly and there appeared to be no irregularities within the object which could be used. Animals showing beating on approaching the walls were marked positive.

Results. From the results (Table 34) it is clear that in the situation described the majority of the animals showed beating ($p < .01$).

Antenna beating - Discussion.

As a preliminary to the discussion it will be convenient to summarise the experimental results diagrammatically. This has been done in Fig. 18. The numbers refer to the relevant experiments described in the text.

The first experiment (expt. 4) had shown that when the insects were presented with vertical objects of different heights and breadths and the use of binocular vision precluded as far as possible, antenna beating occurred at a short and constant distance from the objects. This suggested that the insects were detecting their distance from these objects neither binocularly nor by the apparent object size but by some other means. The hypothesis put forward at this point was that the insects were responding when the base line of the object was seen by the more ventrally directed ommatidia. The results of the subsequent experiments must therefore be considered with regard to whether or not they substantiate the hypothesis.

In brief they do not. A study of the résumé presented in Fig. 18 shows that, as it stands, the idea that the base line alone is responsible for releasing the beating response, is not an adequate explanation of the experimental results. Experiments 5, 6 and 10 do indeed point to the base line as being important for releasing the response. If the base line is raised so that it is not seen by the ventral ommatidia the animals show no response and if a false base line is introduced at a considerable distance from an object the beating starts at that point. Furthermore the beating is shown in response to a horizontal black/white

boundary and starts just before the animal reaches the boundary.

The results of the experiments 7b, 9b and 8 still remain to be explained. In 7b and 9b the base lines are no different from those in 7a and 9a, yet there is no response in the two former while there is a response in the two latter. In experiment 8 there is no base line at all yet a positive response is obtained, this time to vertical black/white edges alone. Now vertical edges are not essential to the response, for they are completely absent in experiment 11, but it is possible that in some cases a vertical object is part of the stimulus situation releasing the response, i.e. that "vertical object + base line" releases the response*. On this basis all the experimental results are explicable except those of experiment 9, experiments 8b and 10 being regarded as special cases where there is a response to the vertical or horizontal alone. The fact that 7b is negative is understandable since, against the white background, the vertical white object is not visible.

The result of experiment 9 is extremely difficult to understand. Experiment 9a is positive although there is no vertical object and, as 9b shows, the horizontal boundary alone is completely insufficient to release the beating. Now in experiment 10, although there were fewer positive responses when the animals walked from black to white than from white to black, there was no doubt that the animals were definitely responding when moving in the former direction, for the number of positive

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* As will be shown presently, the perception of a vertical object does not depend on the seeing of a vertical edge. (See p. 91).

responses was significantly higher than the number of cases where there was no response. It is unlikely that the darkening or lightening of the visual field alone is sufficient to account for the great difference between the results of experiments 9a and 9b. It is possible, however, that since the black area is sharply demarcated against the white background it serves as a distinct object and takes the place of the vertical object in the other experiments in contributing to the releasing stimulus. In view of the evidence it therefore seems that the releasing stimulus is a complex one - "object in front, either horizontal or vertical and appearance of the base line on the lower part of the eye". The distinction between horizontal and vertical objects is not always clear as will be shown below, when the biological significance of the response is considered.

The impression was gained that beating was the more common response to tall vertical objects while dipping (p.83) was seen a little more frequently in response to horizontal ones but no clear correlation was made. In many cases the antennal movement occurred so close to the vertical object that whenever they were brought forward they touched the object and hence it was impossible to say whether they would have been pointed at the floor (dipping) or would have beat horizontally. In the experiments with black/white floors both beating and dipping were observed. It is highly probable that both beating and dipping are two forms of the same general response - "pointing of the antennae with alternate movements" - since in a few cases an intermediate pos-

ition was observed, the antennae beating while pointing slightly downwards but not touching the floor.

The Biological Significance of Antennal Movements as released by visual stimuli.

Although antennal movements, as released by visual stimuli are reported for other arthropods there is an extremely important difference between these cases and the present one for in the former the responses are all to moving visual stimuli. These are either rotating black and white stripes (Wolf and Zerrahn-Wolf, 1935; de Wilde 1940) or single moving objects (Doflein 1910 in Schiller 1937; Buddenbrock 1935, 1952). Furthermore, in some cases, (Bröcker, 1935; Schiller 1937) the object has to be of a certain size to release the response at a certain distance. This was not found to apply in the present case. Many insects respond to rotating stripes by a rigid posture of the antennae (Wolf and Zerrahn-Wolf, 1935; de Wilde, 1940). To a moving object some crabs and other crustacea respond by following the movement with their antennae (e.g. see Buddenbrock 1935; Schiller 1937). In only two of the above cases do the responses reported resemble the antenna beating seen in the present experiments. Eunagarus responds with a blow of its antennae if an object is presented which is large enough to stimulate a group of 7 ommatidia (Buddenbrock, 1935), and if the stimulus is too weak, e.g. small object at a distance, the antennae no longer follow the direction of movement but beat towards the front for a short time and immediately

return to their resting position (Bröcker 1935).

The biological significance of antenna movements as released by visual stimuli has not been discussed by any of the authors mentioned above. To call them "signal reactions" (Doflein, 1910; in Bröcker 1935) is to explain nothing. Bröcker (1935) appears to consider them protective for she says that when the object is just too small or at too great a distance for the crab to consider it dangerous it reacts lazily or not at all. It is almost certain that, in the case of the locust nymphs, as in the other cases mentioned above, the movement of the antennae is an attempt to obtain information about the object by some second sensory modality in addition to that obtained by the eyes. The following of the moving objects with the antennae is merely to interpose the antennae between the object and the animal so that the information can be obtained while yet the object is still at a distance from the animal. The idea of the "checking response" ("sichernde Aufmerksamkeit") has also been suggested in the case of the house cricket Gryllus domesticus L. where the antennae are turned in the direction of a photic stimulus (Federhen 1955).

In Schistocerca it is not yet known which senses reside in the antennae. There may be chemoreceptors such as are believed to be present on the antennae in Locusta migratoria migratorioides (Slifer 1954). The antennae are probably extremely sensitive to bending in different directions as in Locusta (Uchiyama and Katsuki, 1957), and the use of this sense would probably assist the insects to determine more

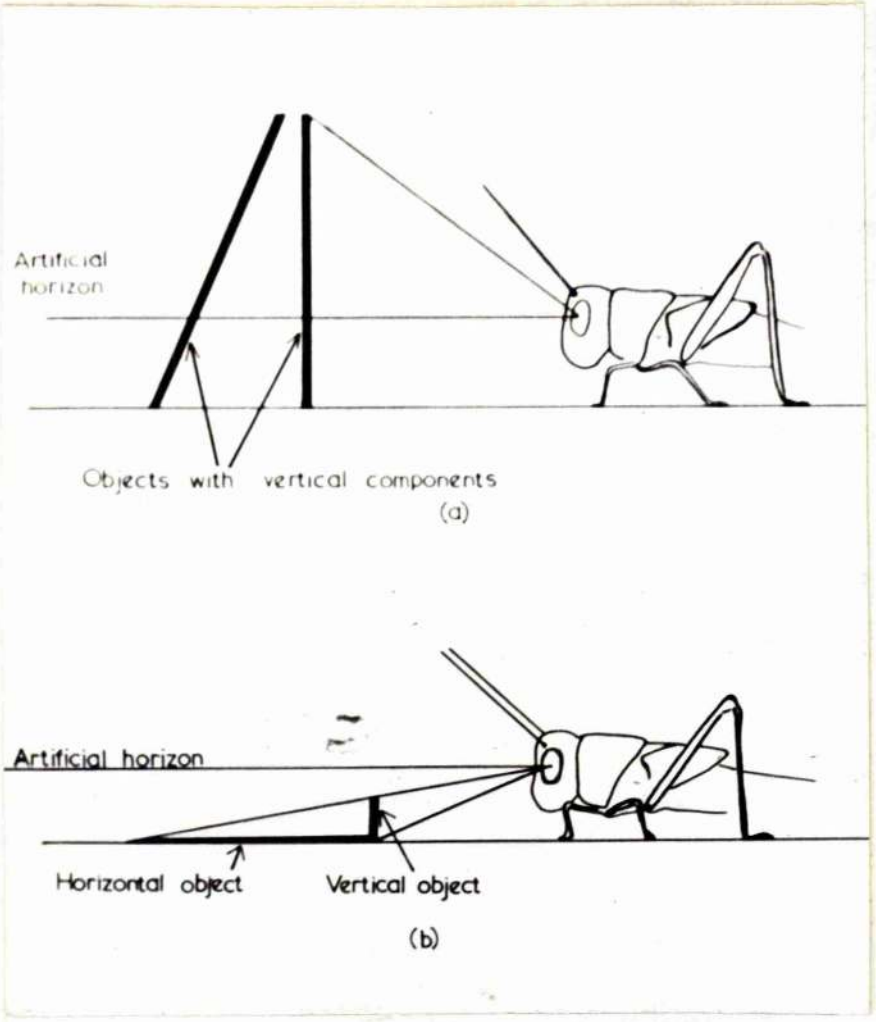

Fig.19.

Diagram illustrating the perception, by an insect, of an object in the vertical plane.

a - unambiguous situation; any object stimulating ommatidia above the line of the artificial horizon must be in the vertical plane.

b - ambiguous situation; either object, horizontal or vertical could stimulate the same ommatidia.

accurately the nature of the object.

Certainly observation suggests that touching the antennae may release a grasping response by the front legs.

At this point it is relevant to consider how a crawling insect can discriminate between horizontal and vertical planes. There does not appear to be any treatment of this in the literature on insect vision.

The question is not how insects differentiate between objects which are completely vertical and those at an angle to the vertical, but the more fundamental problem of how insects detect visually the presence of an upward projection from the horizontal plane, i.e. any object with a vertical component. Man does this by accurate focusing and in the light of his past experience and knowledge of perspective and shading. In the case of insects the first would appear to be impossible and it is hardly likely that the other methods apply (but see Gibson, 1950; Thorpe, 1956, p.130-131). There is, however, one method applicable both to insect and to human vision (and of course in many other cases). This is by reference to an artificial horizon, i.e. the line of sight when the observer is standing erect and looking straight ahead. In insects this is the line of the horizontally directed ommatidia (see p. 26). Any object seen above the artificial horizon must have a vertical component (see Fig.19). An object appearing below the artificial horizon, however, could be either in the vetical or the horizontal plane and still stimulate the same retinal elements, (Fig.19)*.

* This is also true of human vision in certain situations. Personal experience has shown that, in conditions of very dim light, e.g. moonlight, where detailed vision is not possible, it is extremely difficult to determine whether objects lying below the artificial horizon are vertical or horizontal.

It is possible, then, that the antennae are used to give further information about the nature (chemical nature) of an object and that, for objects appearing below the artificial horizon the use of the antennae will tell the animal whether these objects are horizontal or vertical. All of the foregoing will of course also apply to movements of single antennae at the side (flicking).

Antennal movements and distance estimation.

In the introduction to this chapter the possible correlation between antennal movements and distance estimation was mentioned (p. 70). This has not been proved in the case of the antenna flicking (although it may apply; see final discussion p. 116), but in the case of antenna beating it was shown that the insects responded to the base line of the object (p. 78-90). It must, however, be remembered here that the possibility of binocular vision or a "sharpness of image" mechanism (p. 77) operating has not been completely ruled out. If it is true that the insects are using the position of the base line on the eye to estimate their distance from an object it is one of the first instances of insects using secondary cues for distance estimation (see Gibson, 1950 - secondary cues for distance in Man).

RESPONSE TO MOVEMENT.

Introduction.

Many studies of insect behaviour have demonstrated the great importance of movement as a visual stimulus. For example, it is often important in mating behaviour. The pursuit of the female Grayling Butterfly (Eumenis semele) by the male is released mainly by the typical fluttering flight of the female, colour and shape being of only subsidiary importance (see Tinbergen, Meeuse, Boerema and Varossieau in Tinbergen 1951). Movement is also important in the mating behaviour of the butterfly Argynnis paphia (Ilse 1937). The behaviour of many predators involves a response to a moving visual stimulus, e.g., dragonfly larvae only capture moving prey (Baldus 1926); the first part of the behaviour chain of a hunting Philanthus wasp is a response to movement (Tinbergen 1935 in Tinbergen 1951). Mosquitoes show more attraction to moving hosts than stationary ones (Sippell & Brown 1952) and bees are more attracted to moving flowers than to stationary ones (Wolf & Zerrahn-Wolf 1936).

Apart from the work of Ellis (1953) no behaviour study has previously been made of the responses of locusts to moving visual stimuli, despite the fact that such responses are frequently invoked as a basis on which to explain much of the field behaviour (in particular Volkonsky 1942, Kennedy 1951).

Due to time limitations the experiments now to be described must be regarded as merely preliminary to more detailed work.

Fright response to a moving object.

Observation had shown that when a relatively large object, e.g., experimenter's hand, was passed close to a locust nymph the animal "flinched". It was thought that this was possibly a visual response as opposed to a response to air movement or warmth. Fright or fleeing responses released by the sight of movements exist in several insects and arthropods (Baldus 1926, Buddenbrock 1935). An apparatus was therefore constructed for the purpose of studying this response in more detail.

Apparatus. This consisted simply of a long roofless rectangular container with a perspex window at one end behind which a board with a simple black stripe painted on a white background could be moved to and fro. By this means the stripe could be made to pass fairly slowly into and across the visual field with a motion and speed rather like that of the windscreen wiper of a car. When being tested, an insect was seated on a small wooden platform (the same as used for the peering and jumping experiments) placed inside the rectangular container at a certain distance from the window. The inside of the container was completely white and light was from a source 11 ft. overhead and slightly behind the apparatus, thus giving a fairly even illumination of the interior of the box and of the moving stripe.

Animals and pre-treatment. Tests were made with 5th stage nymphs of the normal gregarious phase. The nymphs were kept for 2 hours in jam jars before testing (5 animals to a half-pound jam jar). For the

first hour, they were fed (grass) and for the second they were starved (transferred to clean jars without food). This treatment was an attempt to standardise, at least roughly, the conditions of the animals.

Experimental technique. The animal to be tested was placed on the sloping part of the platform and allowed to walk up it to the end where it would sit quietly facing the window. When the insect was in position, the object was moved fairly slowly to and fro. It was observed that when the object passed the window the insect jerked as if frightened by the movement. In preliminary control tests with the window obscured the insect showed no fright response thus obviating the possibility of a response to noise or vibration. The perspex window of course precluded any interference from air movement.

The object was moved past the window 10 times (5 times in each direction) and the behaviour of the insect noted. If the animal showed any quick distinct movement in response to the passage of the object it was scored positive and the number of positives out of ten totalled. The experiments were repeated at different distances from the object and again with the insects sitting sideways on.

Results. The results are presented in Table 35. As would be expected, the number of responses decreased with distance until at 36" there was only a very faint response indeed. The nature of the response obtained also varied in intensity. At very short distances from the object (9") the insects showed quite large jerks often combined with a "backing away" in which the animal reversed the normal leg-motion

and crawled backwards away from the moving object. In some cases the insect backed the whole length of the platform (6").

At the first passage of the object the insect jerked into a tensed position with the hind legs folded close to the body. Further movements of the object elicited jerks of the whole body in this tensed position and finally the insect might back away, still with the hind legs tightly folded.

When the animals were placed sideways-on to the object, the same jerking, tensing and moving away was noted, the only difference being that the insects did not "back" but moved sideways away from the movement.

At 18" the responses were mainly jerks, "backing away" was much less common than at 9".

At the greater distances (18", 24" and occasionally at 36") it was also noted in some cases that the animals, although jerking in response to the first or second passage of the object, thereafter remained tensed and motionless until the object had ceased to move, i.e., after 10 movements, whereupon the insect then turned round and walked away. This clearly suggests that the insects could see the movement but that it was insufficient to release the fright response and indeed looked as if it might be attractive. It is possible that the same movement when seen close to is "frightening" but as a greater distance is "attractive".

Conclusion. This experiment shows that a "fright response" can be released by the visual stimuli provided by the sudden appearance of a fairly slowly-moving object in the visual field. The insect responds by moving

in a direction directly away from the source of the stimulus.

Optomotor Responses.

The optomotor response is probably the most common visual response to movement. It has been studied in many insects and often in great detail (e.g. Schlieper, 1927; Gaffron, 1933; Hertz, 1934a, 1934b; Gavel 1940; Kalmus, 1948; Autrum and Stöcker, 1952).

It has been demonstrated in locusts by Ellis (1953) who showed that nymphs will march round a gallery following the direction of moving stripes.

The experiments reported below are concerned with the effect of the horizontal movement of a small part of the visual field when seen by different parts of the eye. This obviates the complication of a rotating visual field of 360° which has been used in most previous tests and which has been criticised as representing an unnatural situation in that it never occurs in nature except when the animal rotates on its own vertical axis (Von Buddenbrock 1935; compare also the optomotor response - "a laboratory product" Dijkgraaf 1953 Von Buddenbrock and Moller-Racke 1954).

Stimulus.

In any situation involving a response to a moving pattern a limiting factor is the number of stimulation changes occurring per unit time at any one point on the eye. With moving black and white stripes this is the number of times the stimulation of an ommatidium goes from white to black or vice versa per unit time. It is known that if such stimulus changes follow upon one another too rapidly they are no longer seen as distinct changes and become fixed and the pattern blurred. (Sälzle, 1932) This speed is known as the fusion frequency (Autrum, 1948; 1953, etc.).

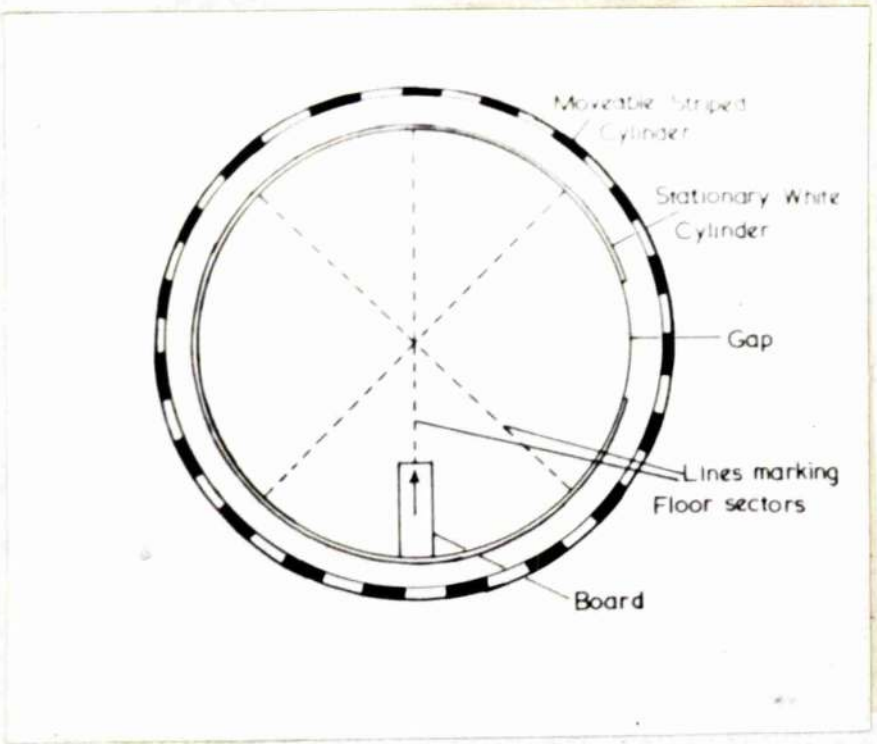

Fig. 20.

Plan view of apparatus used in the optomotor experiments. By means of this arrangement the insects are presented with a movement of stripes over a small part of the visual field.(i.e. at the gap).

It is possible that Schistocerca belongs to the group of insects with a low fusion frequency (See Autrum 1952) and hence, in the present tests, the speed of the stripes was relatively slow and the number of stimulus changes/sec. proportionally small. The fact that the insects did follow the stripes showed that the stimulus had not reached the fusion frequency value.

In the description of the experiments the stimulus will be referred to in terms of changes/sec. and is calculated from the number of stripes and the rotation speed of the cylinder.

The total stimulus received by the insect is equal to the changes/sec. X the area of the visual field over which these occur. In the tests, this was an area of approximately 30°.

Preliminary tests.

The results of these tests were not recorded quantitatively but they showed that the insects would follow the movement of stripes at one side in a situation where these had no rotary component of motion, i.e., the response was not necessarily to a rotating visual environment but to a horizontal movement in one direction. The tests also showed that one eye was sufficient for this.

The effect of a small part of the visual field.

Apparatus and Method. The apparatus used is shown in Fig.20 . By means of this arrangement the insects could be presented with the horizontal movement of the visual field. Light was from a 100 watt bulb 16" overhead. The floor was marked off in sectors as shown.

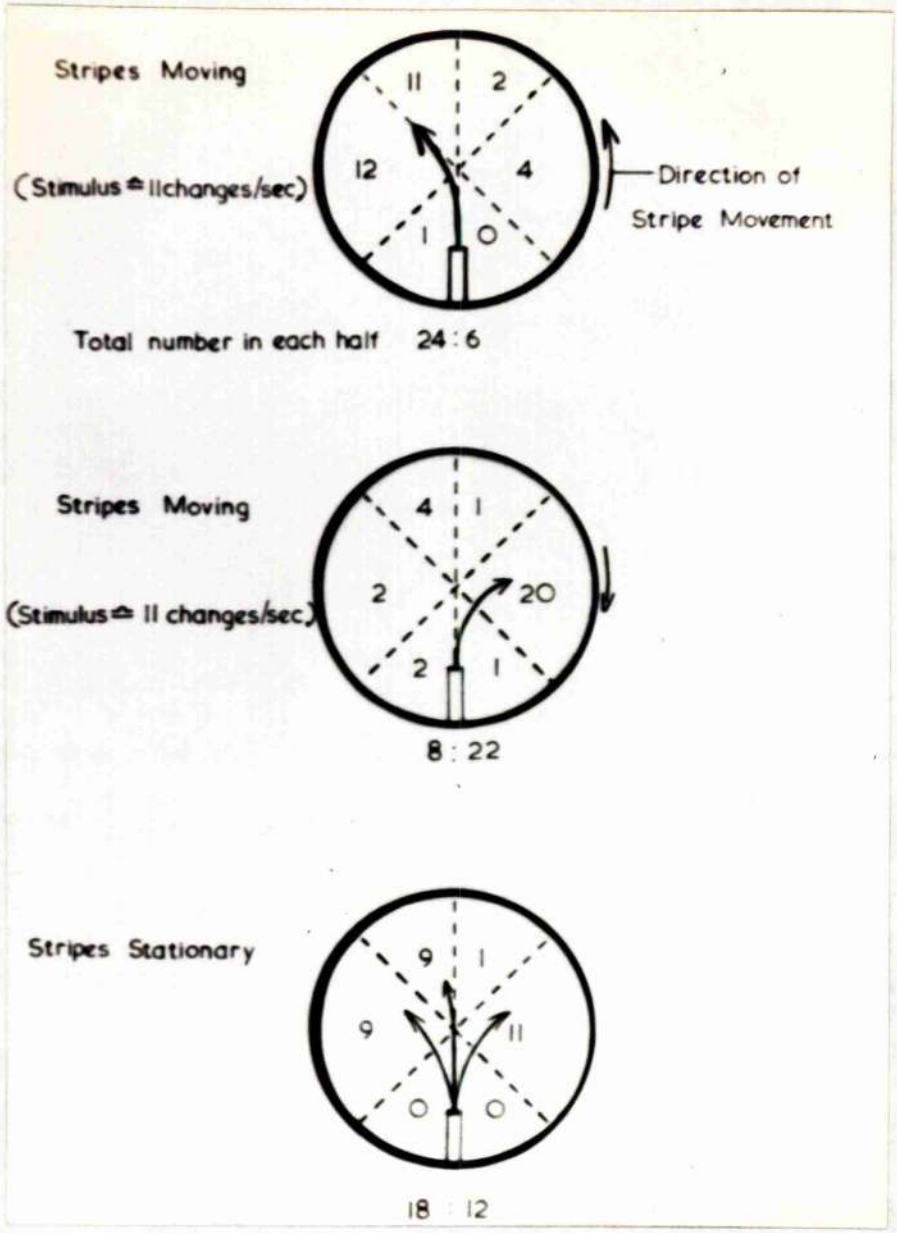

Fig. 21.

Diagram summarising the responses obtained to different directions of stripe movement. The figures represent the total number of visits to each sector in each experiment (i.e. the total for all the insects).

The insect to be tested was placed on the very small strip of wood (1" X 1" section) and allowed to walk to the end. The striped cylinder was then rotated either clockwise or anti-clockwise. The insects were found to walk straight off the end of the stick (since it was only 1" off the floor this was accomplished very easily by the 5th instar nymphs without any disturbance of orientation). Note was taken of the sector into which the insects walked.

In the control runs the cylinder was stationary and a 4" square black object was placed on the wall opposite to the 4" gap.

Results. (Fig.21) The number of animals tested was very small (3 each 10 times) but was sufficient to show clearly that the direction of movement of the stripes had a marked influence on the direction of the animals' tracks. When the cylinder was moving clockwise so that the stripes moved across an animal's right eye from front to rear, the animal turned towards the gap (Fig. 21). When the stripes moved from rear to front of the eye the insects did not approach the gap and tended to walk straight forward, curving slightly to the left (Fig.21). In the controls the animals showed no significant bias ($.3 > p > .2$) to either side (Fig. 21).

Conclusions. The experiments thus show that the horizontal movement of a small part of the visual field has a marked influence on the insects' tracks and that the insects respond to movement over the eye both from front to rear and from rear to front. This last point was confirmed in later tests on unilaterally blinded animals in a rotating striped cylinder

(results not quantitative). The importance of this will be discussed later.

Stimulation of different parts of the eye.

The previous experiment had shown the effect of stimulation by horizontal movement on the lateral part of the compound eye. The animals were now placed facing the gap and tested as before. The cylinder speed was the same as in the previous test.

Results. (Table 36).

It was found that in this situation the animals walked towards the gap quite accurately with little deviation to right or left, although there was a slight tendency to follow the stripe movement.

Conclusion. From the 2 above tests it can be concluded that horizontal movement seen by the lateral part of the eye causes turning but when seen by the front of the eyes has less effect.

Importance of the Type of Movement.

Apparatus. The animals were again placed facing the gap but this time the rotating cylinder was completely white except for 2 black stripes 4" broad diametrically opposite. The rotation speed of the cylinder was 1 rev./2 secs. hence the stimulation equalled 2 changes/sec. (intermittent; long white period short black period). A control was performed with the cylinder stationary.

Results. It was found that the intermittent stimulus supplied by the 2 moving stripes elicited the fright response (jerking with slight backing). The results are presented in table 36 line 3 and show that in the majority of cases the fright response was observed and that

the insects rarely approached the gap. In many cases they sat still or turned round on the stick without showing any response at all to the movement.

Conclusion. Comparing the above results with those obtained when the cylinder is completely covered with 1" black and white stripes (previous experiment) shows that these 2 types of movement when seen by the same (front) part of the eyes elicit different responses.

Optomotor Responses - Discussion.

The preceding experiments have thus shown that the same movement (of stripes) produces different responses when seen by different parts of the eye. Different movements produce different responses when seen by the same part of the eye. Furthermore the portion of the visual field occupied by the movement does not need to be large ($\simeq 30^{\circ}$) and the animals respond to movements of shape over the eye both from front to rear and from rear to front.

It is interesting to compare these results with what has been found for other insects. Thus locusts follow the direction of stripe movement (when seen on the side of the eye) whereas some insects walk so as to oppose the stripe movement.(e.g. bees, Hecht and Wolf, 1929). Again, while the lateral portion of the eye is the one involved in the optomotor response in locusts and many other insects, it is the anterior part of the eyes which is important in Mantis (Schlieper 1927) and in some cases the moving part of the visual field has often to be larger (Schlieper 1927) than for locusts. Finally, some insects show little or

no response to a movement over the eye from front to rear, e.g., Aeschna nymphs (Tonner 1938) and the weevil Calandra granaria (L.) (Buddenbrock & Moller Racke 1952). Since the response in locusts was not measured quantitatively it is impossible to state whether or not the insects respond equally well to movements front to rear and rear to front, but it is nevertheless clear that a response to movement from front to rear does exist in Schistocerca.

The facts mentioned above, particularly the response to movement over the eye from front to rear, are of great significance to the problem of the differentiation of subject and object movement which is now to be discussed.

Subject and Object Movement.

The movement of an image of an object over the retina depends on the relative motions of object and animal*, (for animals with unmoveable eyes). There are a whole series of conditions ranging from the situations where both object and animal are moving to the extremes which are:-

1. Object moving animal stationary
2. Object stationary animal moving.

As Buddenbrock states (1952) these situations are fundamentally different. It is therefore necessary in any discussion on responses to movement, to

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* This does not include the phenomenon of stroboscopic vision which is known to exist in insects (e.g. see Autrum 1952).

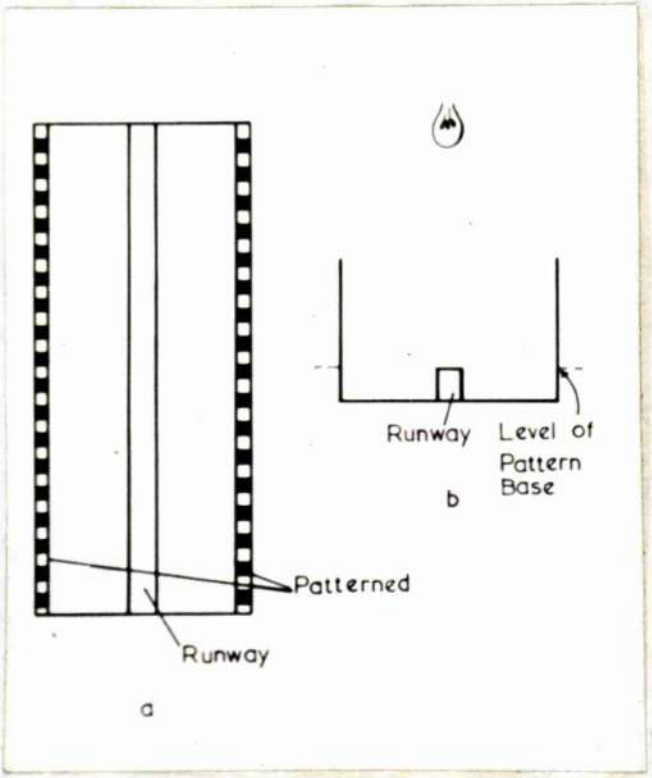

Fig. 22.

a - plan view and b - end elevation of apparatus used in the von Buddenbrock experiment to measure the relative attractiveness of different striped patterns.

distinguish sharply between the two. In the present work it is proposed to refer to the first situation as one involving "object movement" and to the second as "subject movement". So far, therefore, the experiments described in this section have been concerned with responses to object movements.

The experiments on form perception and peering have clearly suggested the importance of subject movement as a stimulus, the following experiment was undertaken with the aim of enlarging upon this.

The Von Buddenbrock Experiment.

The experiment to be described is a modified version of a test carried out by Von Buddenbrock (1935) (Von Buddenbrock and Moller-Racke 1952a) to investigate form perception in Eristalis tenax (L.). In it the insects are made to walk down a corridor with patterned walls and note is taken of the side to which the insects deviate.

Apparatus. The apparatus used in the present tests is shown in Fig.22 and differs from that of Buddenbrock in having the light overhead instead of at the end of the corridor and in confining the insects to walking along a runway instead of on the floor. This latter arrangement served to keep the insects at a known distance from the wall. Each wall was completely covered with a certain pattern and the experiment carried out for several different patterns.

Procedure. The animals were placed on the runway and allowed to walk down its length. Animals either walked down the centres of the runway or with the body obliquely across the runway with the head nearer

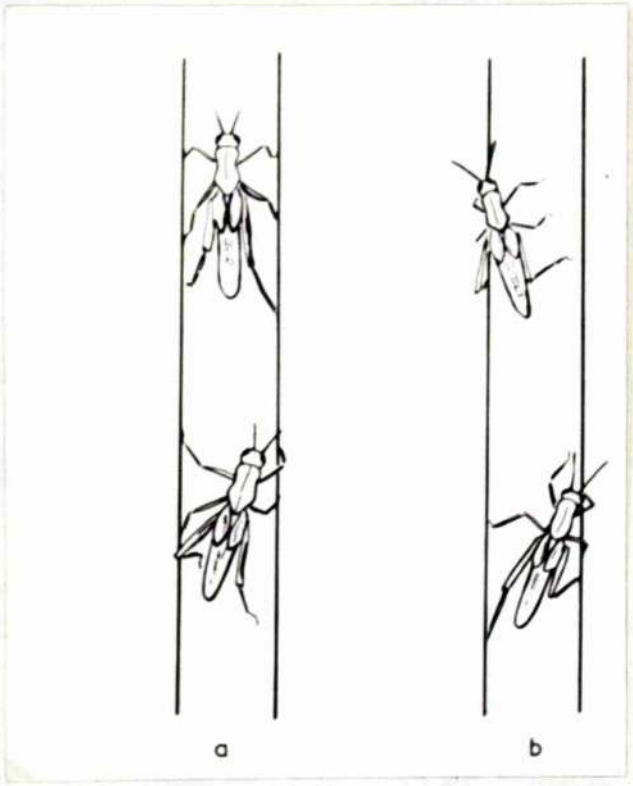

Fig. 23.

Positions taken up by locust nymphs walking along a horizontal runway between patterned walls.(see text and Fig. 22).

a - insects in"centre" position;head in centre of runway or <u>not</u> at the edge.

b - insects in "left" and "right" positions;head touching the edge or over it.

one side than the other. The meaning of the terms "right" "left" and "centre" positions are shown in Fig.23 By means of a pendulum, so situated that the observer could watch its oscillations without taking his eyes off the walking insect, readings were taken at regular time intervals (every 1.5 secs).

Results. The results are presented in table 37 . They can be summarised as follows:-

Test Series 1. When the insects were placed equidistant from the walls with identical pattern (1" wide black/white stripes 8" tall) they showed no bias to either side.

When the insect is twice as far from one wall as from the other the bias is towards the nearer wall, i.e., the insect runs down the runway with the body slanting across obliquely and pointing to the nearer wall.

Test Series 2. When placed equidistant from two equally fine patterns (1" black/white stripes) one of which has stripes twice as tall as the other, the insects deviate towards the taller pattern. However when placed so that their distance from the taller pattern is twice as great as the distance from the shorter pattern (both patterns now appearing to be of equal height) the insects deviate towards the nearer pattern as in Test Series 1.

Test Series 3. When placed mid-way between two equally fine patterns, one of vertical stripes, and the other of horizontal stripes* the insects

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* The patterns were so arranged that each contained the same and equal areas of black and white and the length of the horizontal black/white contour of one equalled the length of the vertical black/white contour of the other.

deviate towards the vertical stripes.

Test Series 4. Animals running between two patterns, one twice as fine as the other, at equal distances from each, deviate towards the finer pattern. (1" vertical stripes as opposed to 2" vertical stripes).

Discussion. The results obtained in the present experiment differ from those obtained by Von Buddenbrock (1935) and Von Buddenbrock and Moller-Racke (1952a) on several major points. Thus, Von Buddenbrock (1935) concluded that the basis of attraction to form in Eristalis did not lie in any response to retinal movement but in a response to a stationary pattern. He found that his insects, when placed between a horizontally striped wall and a vertically striped wall, deviated equally to either side and, if anything, showed a slight preference for the horizontal, although, for a horizontally crawling animal, the vertical contours must produce more image movement over the retina. The present tests (Series 3) have shown that, in such a situation, locust nymphs deviate consistently towards the vertical contours, thus emphasising the importance of these contours and hence of the retinal movement and substantiating what had been previously found in the form perception and peering experiments.

Next, Von Buddenbrock (1935) states that in responses to striped patterns only two variables are important, the stripe breadth and the distance between the stripes. Since he has concluded that the movement of stripes over the retina is not important he therefore omits to consider the effect of the distance of the animal from the pattern and thus the speed at which the patterns will pass over the eye. This omission

leads him to put forward an over-simplified explanation of the behaviour of an insect in a stationary striped arena. He states that as the insect approaches one wall the pattern on the further wall becomes finer and hence more attractive and causes the animal to turn*. While his experiments clearly show the importance of fine-ness and the present experiments confirm this (Test Series 4), these latter also suggest that the speed of movement is important. In Test Series 1 it was found that, when running between two identical patterns but twice as close to one as to the other, locust nymphs deviated towards the nearer pattern. This pattern is apparently coarser than the more distant one yet it is more attractive and it is very possible that this is because its components pass over the eye more quickly than those of the more distant pattern. The attraction to the nearer pattern is not due to the stripes being apparently taller than those of the more distant pattern (Series 2) although tallness does appear to have some effect when the animal is equidistant from both patterns and the speeds of stripe displacement over the eyes are equal.

Conclusion.

This experiment has thus shown that, contrary to the case of Eristalis, in the case of Schistocerca the attraction to a pattern can be

* In further papers (Buddenbrock and Moller-Racke 1952b, 1953 1954) on a slightly different topic he does bring in apparent movement as an important stimulus.

adequately explained as a response to stimulation through movement of retinal images. Besides, therefore, the two variables stripe breadth and distance between stripes which Von Buddenbrock found to be important there can clearly be a third important variable (at least for Schistocerca). This variable is the distance of the insect from the pattern. These findings are therefore in complete agreement with the results of the form perception and peering experiments in which the importance of stimulation due to movement of contours over the retina was revealed.

The differentiation of subject and object movement.

At first glance it would seem that insects must certainly differentiate between the different causes of image movement. It is true that the stimulation of the retinal receptors will be the same in either case, for the same image movement will occur whether an insect walks past a stationary object or an object moves past the stationary insect. One would expect however that the CNS would differentiate between the two situations. It has proved, however, far from easy to demonstrate this in a convincing way experimentally. At present there are two schools of thought on the subject. Buddenbrock and his co-workers believe that in many cases insects do not distinguish the one situation from the other (e.g. Tonner, 1938, Buddenbrock and Moller-Racke 1952a, 1952b, 1953 1954). while Hertz (1934), von Holst and Mittelstaedt(1953), Mittelstaedt(1952), von Holst(1954)(~~A.S.A.B.~~) and Dijkgraaf(1953) believe that they do. Both sides have put forward experiments to justify their claims but in every case weaknesses in the experimental set-up have been criticised by the

opposing side.

Buddenbrock claims (Buddenbrock and Moller-Racke 1952b; 1954) that the weevil Calandra granaria (L.) only responds to movements over the eye from rear to front and not from front to rear. As he correctly points out, this would solve the problem for this particular insect. It does not require to differentiate between subject movement (which is always front to rear except when the animal walks backwards or turns) and object movement since it just does not respond. (See also Aeschna nymphs, Tonner 1938). However, it has already been shown (p.99) that locust nymphs do respond to stripes moving from front to rear of the eye, so that in this case the insect is faced with the problem. The following experiment was an attempt to show that locust nymphs could differentiate between the two situations.

Principle.

The general principle of experiments relating to the above problem is to provide two situations in one of which the surroundings are moving and the animal stationary, while in the other the animal is moving and the surroundings are stationary. It is a prime requisite of this type of experiment that the two situations be exact opposites of one another. It is then noted whether or not the animal behaves in the same way in both situations.

It is felt that, in the present experiment, the above conditions have been fulfilled to perhaps a greater extent than in previous experiments of that type. Use was made of the fact that nymphs of Schistocerca

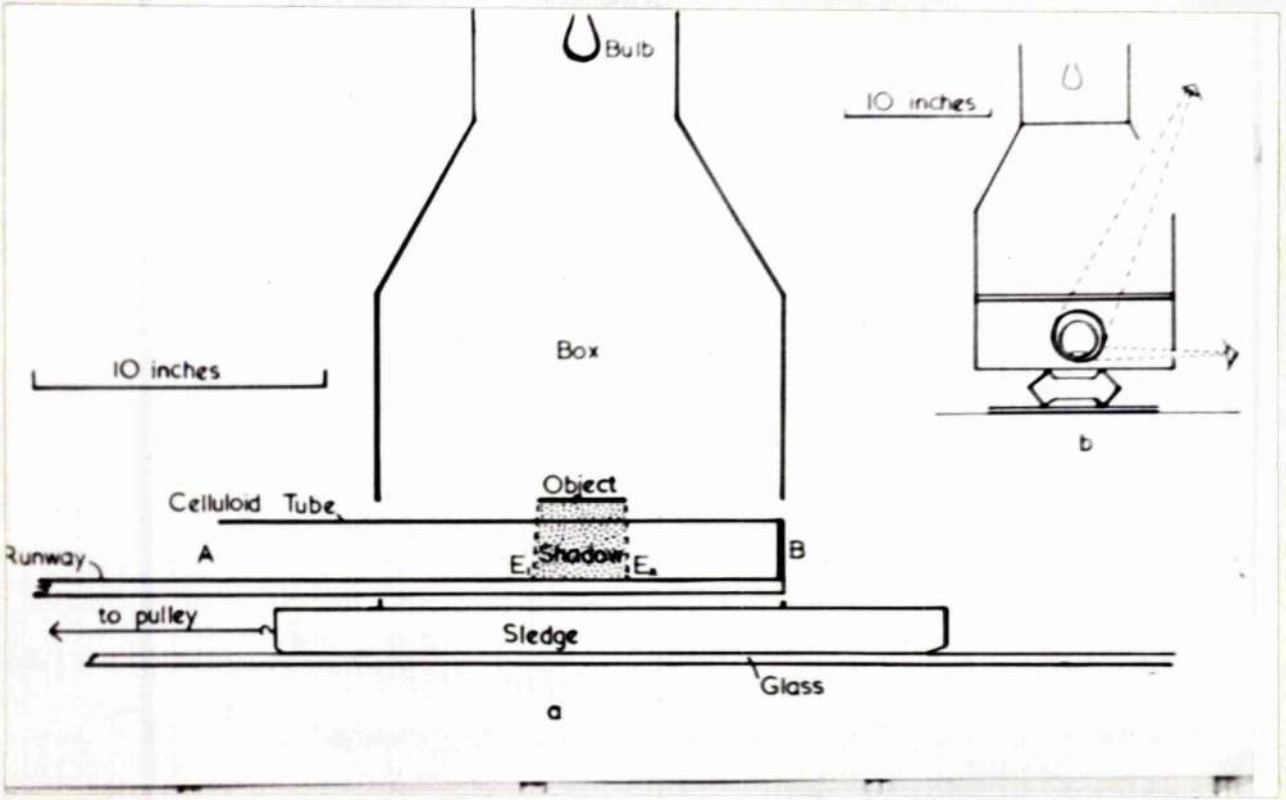

Fig. 24.

a - Side elevation of apparatus used to test the ability of locust nymphs to differentiate "subject" and "object" movement.
b - End elevation showing two positions from which insects could be observed.

show the fright response (p. 94) when an object or a shadow passes over them.

Apparatus. This is shown in Fig. 24 . It simply consisted of a square box of side 14 ins. and height 18 ins. sitting on a wooden sledge. The box was illuminated by a 25 watt bulb 21 inches directly overhead surrounded by a black shade so that the walls of the box were slightly less illuminated than the floor. This arrangement stopped the animals from making repeated attempts to jump onto the wall and climb up to the light. The sledge, box and lamp, formed one complete unit which could be moved very smoothly as shown in the diagram, the sledge sliding over a glass surface. There was a stationary, narrow, wooden runway surrounded by a transparent cellulose tube (2 1/2 ins. dia.) which was fastened to it. This tube had an open end at (A) and an opaque closed end at (B). The object was a piece of black cardboard 3 ins. broad and running from one side of the box to the other at right angles over the runway on which it cast a shadow. This object was fastened to the box so as to move with it. A small slit, cut in the side of the box under the object allowed the insect to be observed even when under the object. Fig. 24b shows the 2 positions from which observation could be made.

Experimental conditions.

(1) Apparatus stationary; animal walking.

In this case the animal was placed on the runway near (A) and allowed to walk into the box and right along the runway to the other end, passing under and through the shadow. It was found that an animal usually stops

at least once during this journey. The apparatus was completely stationary.

(2) Apparatus moving; animal stationary.

The animal was again introduced at (A) and allowed to walk into the box. Whenever the insect stopped temporarily (as in the previous situation) the complete unit of the sledge etc., was pulled in the direction shown by the large arrow in the figure. In this way the whole of the environment was made to pass a stationary animal and the object (O) to pass over it. The runway etc., remained stationary.

Speed. The speed at which the insect made the journey in the first situation was measured with the aid of a stop-watch and in the second situation the apparatus was moved at approximately this speed. The speed was usually in the region of 1 inch per second.

Animals. The animals used were 5th instar nymphs which were well fed beforehand. Each was tested several times in both situations. To obviate the influence of increased excitement as the test progressed the order of presenting the situations was varied.

Behaviour.

(1) Apparatus stationary. In almost all cases (46 out of 52) the insects walked straight along the runway to the end, passing under the shadow and out again without turning back. In one case the insect stopped completely for a long period when under the shadow and in the other five cases the insects turned aside and climbed on the wall of the tube,

either when at the first edge of the shadow (E_1), when under the shadow, or when at the second edge (E_2). The insects usually paused whenever they entered the lighted box but, apart from this, several (15 out of 52) paused when they reached the first edge of the shadow. Pausing was also seen in some cases (19 out of 52) when the second edge was reached. Few animals actually paused underneath the shadow.

Antennae waving or dipping was occasionally seen in response to the first shadow edge (15 out of 52) but was rarely seen under the shadow or at the second edge. Some insects waved their antennae for the whole length of the runway.

No jerking or backing was ever seen in response to the object or shadow or indeed at any time during these runs.

(2) Apparatus moving. In sharp contrast to the behaviour described above in more than half the cases (37 out of 62) where the surroundings and the object were moved past a stationary animal a fright response was observed. This was either a slight jerk, a violent jerk back, or, in a very few cases, a walking backwards. In four cases the insects, after jerking and backing, turned round as the object moved over them. The fright response usually occurred when the first shadow edge reached the insect but in a few cases there were also jerks while yet the object was at some distance from the insect, e.g. at one or two inches. In eleven cases the insects sat motionless while the object passed over. In yet another case the insect, which was sitting still, merely twitched its antennae slightly as the edge approached. In two cases the insects

tried to climb on the wall of the tube. Finally in eleven cases the insects were walking when the object passed over them, in some cases having just started to walk forward when the object was close to them. Only one walking insect, moving very slowly showed a fright response.

Results. The results of the experiment are presented numerically in Table. 38.

Control.

The only factors which could perhaps have given rise to the fright response, apart from the obvious visual factor, was ground vibration. Any influence of air vibration had been prevented by the cellulose tube surrounding the runway. It was possible, however, that although the apparatus apparently moved very smoothly there might be some vibration of the bench on which it was resting. The control experiment was to evaluate this possibility.

Apparatus. In this case a short runway with a cellulose tube was fastened to the floor of the box so that the complete apparatus moved as one unit. Box, insect and shadow are all moved together.

Technique. The insect was placed on the runway and allowed to enter the box. Whenever it had paused the apparatus was moved smoothly as in the previous experiment at a speed of approximately 1 inch per second.

Behaviour. No fright responses were observed (out of a possible 20). In eight cases the insects sat perfectly still the whole time and in two of these (both different animals) they started to walk when the apparatus had stopped. In ten cases the insects walked the whole

length of the runway, pauses and antennae movements being occasionally seen. (Cf. the test with the stationary apparatus). In a further two cases the insects first walked and then paused underneath the shadow and were still there when the apparatus stopped.

Conclusion. It is clear therefore that, whatever other effects ground vibration may have had on the behaviour of the nymph , its presence did not produce a fright response. This was only produced when the moving object, casting a shadow, passed over a stationary insect.

The differentiation of subject and object movement - Discussion.

The literature on this subject is very confusing and there has been at least one large, accidental and irrelevant digression on the subject of the compensating movements of eye stalks in Crustaceans. After lengthy discussion (Buddenbrock and Moller-Racke 1953 , 1954; Dijkgraaf 1953) as to whether or not experiments involving this response proved that these animals could differentiate between subject and object movement, it was finally found that the response was not a visual one at all but correlated with a rotation sense situated in the thread hairs of the statocysts (Dijkgraaf 1955a, 1955b).

Both parties at one time or other have emphasised that the optomotor response is an artificial laboratory product (Dijkgraaf 1952; Buddenbrock and Moller-Racke 1954) and yet it is nevertheless used in experiments on the subject (see Buddenbrock and Moller-Racke 1954). In a striped rotating cylinder the movement of the stripes is in the opposite direction over the twoeyes of the animal whereas, when the insect is walking, the

movement is in the same direction over both eyes (although it may be faster over one eye than the other when the insect makes a gentle curve). It is Buddenbrock's opinion that, in the natural situation, these movements will usually balance one another and the animal will walk straight. A little reflection will show that the only natural situation equivalent to the rotating cylinder is when an insect rotates on its own axis at the centre of a stationary cylinder. All experiments therefore in which the insects are not confined to the centre are invalid (e.g., some of the experiments of Hertz 1934; Tonner 1938; Buddenbrock and Moller-Racke 1952).

Finally it is very difficult to detect the difference between two intensities of what might be the same response. For example an animal walking in a curved path in a stationary cylinder and walking in a more circular path in a rotating cylinder (Buddenbrock and Moller-Racke 1952 b).

It is felt that the present technique has removed many of the above difficulties. The "movement" of the surroundings which occurs when the animal walks past them is exactly the same when the surroundings are moved past the stationary animal (except that the runway on which the animal sits remains stationary). The use of a horizontally moving apparatus precludes the complications of a rotating cylinder. Finally the sharp distinction between the behaviour in the two situations shows quite clearly that to the insects these are completely different. The objection could be raised that the insects were merely responding to a sudden change in light i tensity (i.e., not to a movement). However, the fact that in several cases the insects showed the fright response before the shadow

reached them (distance varying from 1/2 inch to 4 inches) makes this unlikely. It is most possible that the response in many cases is to a movement of a light intensity change over the eye. In such cases the action of the light intensity change does not invalidate the argument for it is immaterial whether the animal reacts to a moving shadow or to a moving object. It is still differentiating this from the "movement" which occurs when it walks under the stationary object.

The present experiment contributes no evidence as to the actual mechanism whereby the insect differentiates the two situations. Such a mechanism has, however, been postulated for other cases (Von Holst and Mittelstaedt, 1950) and this will be discussed in more detail in the General Discussion (p.116).

Response to Movement - Discussion.

Since the various responses have been discussed fully individually it only remains to re-iterate here the three main points which have emerged.

1) There are various responses to movement of objects in the environment (object movement).

2) There is also a response to the stimulus supplied by subject movement.

3) The insects seem able to distinguish between subject and object movement.

GENERAL DISCUSSION.

In the present investigation, locust nymphs have been presented with relatively simple visual environments consisting of two-dimensional black areas on white backgrounds. In such situations it has been found that the insects are spontaneously attracted to the black areas, can differentiate between the shape of these "objects", estimate their distance and react differentially to different movements. Notwithstanding the apparent diversity of these responses it is possible that they are all, in the main, responses to the stimulation produced by contours moving across the eye. Thus, as has already been proposed (p.41 et seq.) the attractiveness of a shape may be explained to a great extent on the basis of stimulation through contour movement. It has been demonstrated that the insects estimate distance by measuring the amount of displacement of images over the eye. It has been shown also that the deviation of the insects to right or left in the Von Buddenborck experiment can be related to the amount of stimulation received from either pattern as a result of its motion across the eye. This is in turn related to the number of contours and their speed of "relative" motion. Finally, although it has not been demonstrated experimentally, it is possible that the antenna flicking (not the beating) when a nymph passes an object at the side is also a response to the "motion" of the object's contour. Thus, at a distance, the amount of relative movement would be too small and the

insect would not respond, a faster speed of movement would tell the insect that the object was close - at this point the antenna could be profitably extended in that direction for the receiving of new information. It was indeed observed that antenna flicking only occurred at fairly short distances from an object (up to 5 inches). Furthermore, it is extremely suggestive that the flicking should occur when the object image passes to the more lateral part of the eye (60° - 70°) for at this position it will have greater speed of displacement than when in front of the animal, the greatest speed being attained when the object is at an angle of 90° to the insect.

It is well known that the insect apposition eye is extremely well adapted for the perception of movement. It can perceive movements of extremely small magnitude (Burtt & Catton 1954, 1956), very slow movements (Mittelstaedt 1952) and in many cases very fast movements (Autrum 1948, 1952). It would not be surprising therefore to find that the movement of ~~part~~ images on the retina played an important role as a stimulus. This point has be n made by several workers, ((see Bibliography), Hertz, Autrum, Wolf & Zerrahn Wolf.)

Since it can be held that object images are seldom if ever completely stationary on the retina, there being always slight movements of the receptors, it might at first appear merely a truism to say that any insect, or indeed any animal, is responding to movement. However, there must be a clear distinction made between the situation in which movements of the receptors are merely employed to scan the object in question (Eye

Ball movement in Man, Ditchburn & Fender 1955, Ditchburn 1955, Scanning movement of head in Caterpillars, Dethier 1943), and the animal then responds to further qualities of the object seen and the situation in which the animal responds directly to the movement-stimulus. That is, the stimulus immediately signifies "attractive shape" or "near object". Hertz (1935) said that it was merely academic and premature to separate movement vision, form vision and spatial orientation. On the one hand she may have meant only that the same basic physiological principles were involved in these cases, on the other hand she may have meant that the responses to these stimuli were basically similar.

In the present investigation the simple nature of the objects involved may have unduly emphasised the importance of contour movement since the effect of other properties such as colour and three-dimensionality have not been assessed. However, this may only mean, at the most, that the system whereby the insect responds to contour movement is only one system operating amongst several. As will be mentioned later, it may be a relatively primitive system but this does not preclude its being the important one even in the presence of other stimuli. Thus Hertz (1931) found that even in experiments with three dimensional objects the bees reacted to the patterns of light and shade i.e. to black and white contours. It is therefore proposed to consider further the properties which such a system would possess, and the sort of behaviour which might be expected as the result of these properties. The discussion will be couched in

general terms, for it will apply to all compound eyes, but the points will be illustrated with particular reference to the behaviour of locust nymphs wherever possible.

Total number of ommatidia stimulated and speed of image movement.

When a locust nymph sways its head sideways in peering the images of the objects in the environment move across the retina. It has been shown that the nymphs use the speed of image movement as a measure of object distance. It might, at first, appear that this speed was equal to N/T where:

N = number of ommatidia stimulated and
T = the time for the head movement.

It would not require a very complicated nervous mechanism to evaluate these quantities. Further reflection shows, however, that the problem is not quite so simple for the quantity N depends on several factors. As well as depending on the distance of image displacement over the eye (d) it also depends on the lengths of the moving contours (L) and the number of contours (C). Thus N is proportional to L X C X d.

If then the insects were to estimate speed and therefore object distance by measuring N/T they would confuse the distances of tall and short objects (since L would be different in each case) and also the distances of plain and striped objects (since C would be different in each case). Now it has been shown that locust nymphs do not confuse the distances of tall and short objects, they prefer the nearer object and jump on it (i.e. they measure its distance accurately.) As for striped and

unstriped objects, while it is true that the insects show a slight preference for a more distant striped object as against a nearer plain object, they still jump on the chosen object accurately. It is clear therefore that they do not estimate distance as simply proportional to N/T but measure the distance which the whole image traverses over the eye.

The stimulus effects of L and C have this in common, that when a long-contoured, or a many-contoured figure moves over the eye, there are a large number of simultaneous discharges from different ommatidia. In the first case a whole vertical row fires together, in the second, both vertical and horizontal rows fire together.*

The operation of the peering mechanism, therefore, could be postulated thus. The insect starts to move its head and batteries of ommatidia discharge. This informs the insect of the nature and extent of the figure. When the head has reached its limit of sideways traverse the whole pattern of discharge has moved to a new group of ommatidia. The extent of the movement is proportional to the distance away of the object.

Attractiveness of objects.

It has been shown, that, for locust nymphs, two properties influence their spontaneous choice of figure. These are the shape of the figure

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* For oblique contours oblique rows of ommatidia will fire together, but an oblique figure may be satisfactorily classified in terms of vertical and horizontal axes.

and its nearness. It therefore appears that sometimes the insects are responding to the number of ommatidia stimulated i.e. $N \propto L \times C$. (d is not important if the objects are at the same distance), hence the importance of length and number of vertical edges and of articulation. At other times they apparently respond to the quantity d. When the objects are at equal distances or when the difference in distance is not great then d will be unimportant and the shape of the object will exert most influence.

Speed of image movement and position on the eye.

The speed at which an image moves over the retina varies with the direction of the object with respect to the movement of the receptor*. When an object is at right angles to the line of movement of the receptor its image has the maximum speed of movement. Thus for a walking insect this position is to the side of the animal and for a peering insect it is in front.

If the insect is to use the image displacement as a measure of distance either for jumping or for antenna-waving this complication of direction must be resolved. It is possible to conceive of a central nervous system which integrates the position of the image on the eye and its speed

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* It was for this reason that in the peering and jumping experiments great care was taken to position the two objects so as to appear on identical parts of the two eyes - 45° to each side of the 0° line.

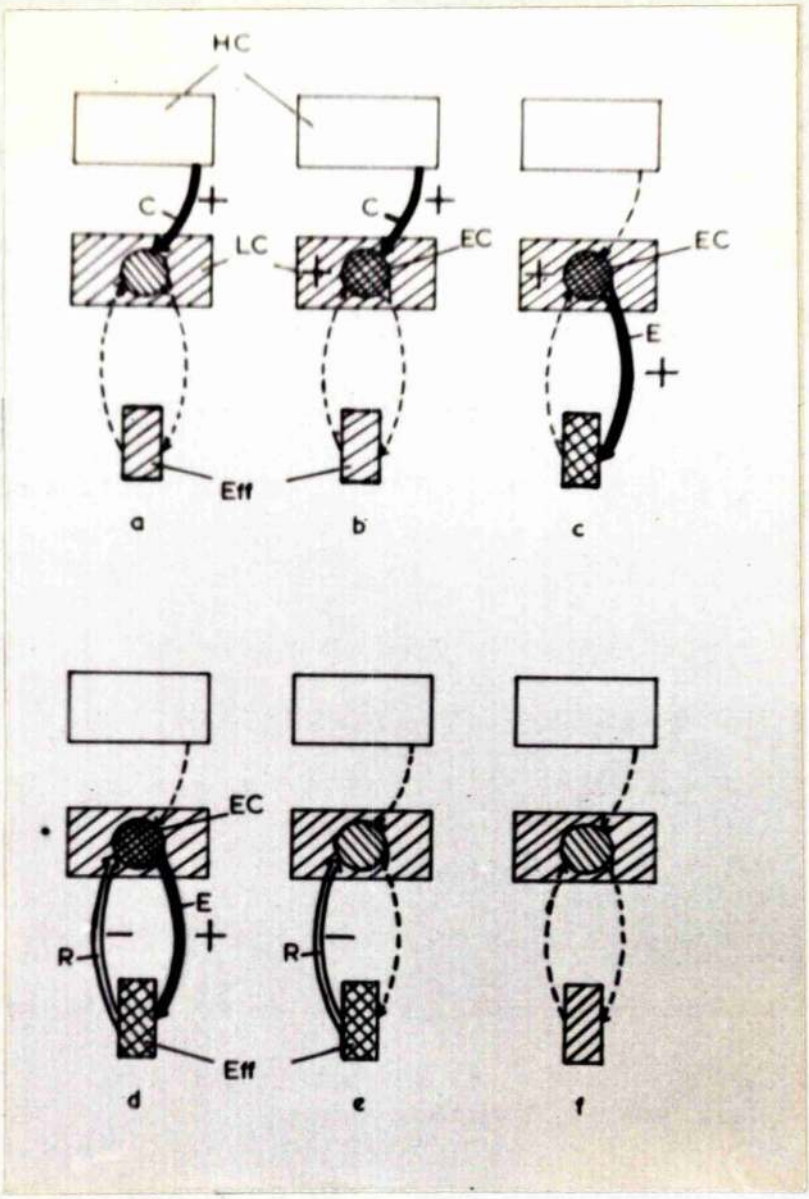

Fig. 25.

Diagram illustrating the re-afference principle.
Time series a - f. HC - higher centre, C - command,
LC - lower centre, EC - efference copy, E - efference,
Eff - effector, R - re-afference. For description see text.
(from von Holst 1954)

of motion but this is perhaps unnecessarily complicated. As an alternative the insect can respond to the image movement when it is at its maximum, i.e. when the object is at 90°. The following facts support this. The antenna flicking occurs in response to an object on the more lateral part of the eye. In the peering experiments the insects turned and faced the chosen object and then peered again before jumping. It is of course possible that in many cases the insect is not intent on discovering the nearest object, in which case it might just peer and then walk towards the region of greatest stimulation.

Subject and object movement.

The problem of differentiating between subject and object movement has already been mentioned (p.107) and the experimental results appear to show that locust nymphs can solve this problem. A theoretical system has already been proposed by former workers to explain how animals can differentiate between the two situations. This is the "Re-afference Principle" ("Das Reafferenzprinzip" Von Holst and Mittelstaedt 1950).

It is not proposed here to go into a detailed exposition of this thoery, which can be stated briefly as follows. (See Fig.25). A motor impulse (c) from a higher centre (H.C.) causes a specific activation of a lower centre (L.C.) which in response gives rise to a specific efference (E) to the effector (Eff.) e.g. muscle. The specific activation in the lower centre, i.e. the "image" of the efference, is the "efference copy". The effector activated by the efference moves and produces a "re-afference" (R) which returns to the lower centre and

nullifies the efferency copy by superposition. The efferent part of the process can be designated + and the afferent part as -. When the re-afference is equal (and of course it is opposite) to the efference copy these exactly compensate one another and nothing further happens. (After von Holst 1954). Thus it has been shown that when an insect moves freely in a stationary striped environment the stripes do not appear to move (Mittelstaedt 1952). A central command, e.g. move to the left, leaves an efferance copy which is nullified by the re-afference caused by the displacement of images over the retina and thus the objects do not appear to move.

Now, for the present discussion, the important point is this, that it is difficult to see how, in some cases, the efference copy and the re-afference can be completely balanced. It has been repeatedly stressed in this discussion that when objects are at different distances their images move over the retina at different speeds - the closer the object the faster the speed - and none of the images will be displaced with a speed equal to or faster than the insect's movement. In order, then, for there to be no illusion of object movement the system must compensate for the whole range of image displacement. Now, this would be a very complex process even if the insect had some independent means of measuring distance, since the information as to the object distance would have to be fed into the system via the receptors and integrated with the different rates of image movement. However, if the insect in the first place measures distance by image displacement, as locust nymphs apparently do

(at least for fairly distant objects), the information as to distance is not forthcoming until the movement is performed. Furthermore, if some of the objects start to move slowly as the insect moves their movement will not be perceived. They will merely appear closer or more distant depending on the direction of movement. Hence the result of the peering and jumping experiment with a moving object. (p. 65).

There will, however, be a speed of displacement which cannot be exceeded by the image of any stationary object and that is the speed of the insect's own motion at the time, i.e. the speed of the peering movement or of walking. It could therefore be postulated that when the insect is moving the speed of this movement is transmitted to the central nervous system and any object whose image displacement is less than this will be seen as stationary. Any object whose image speed exceeds this must be moving (and in the opposite direction to the animal). For an object moving in the same direction as the animal its smallest displacement can be zero, i.e. it must be moving at the same speed as the animal. This would represent an object at infinity. It will be perceived as moving if its speed is greater than that of the insect.*

On the above hypothesis it is likely that a walking insect would not respond to the movement of an object which was moving slowly but if the object were moving in the opposite direction to the insect the latter might react to it as if it were a very near object. In several cases the ob-

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* Consequently objects moving in the same direction as the animal can attain a greater speed of movement than those moving in the opposite direction to the animal without the movement being perceived.

served behaviour of the locust nymphs suggested this. In the experiment with the moving object and shadow walking animals often waved their antennae and showed attempted clasping as to a near object. Furthermore, only one walking animal showed a fright response and that animal was walking very slowly. This strongly suggests that the other walking animals did not perceive the object as moving. In the case of the slow insect it is probable that the object speed was in excess of the insect's speed and the motion would be perceived. When an insect is stationary all movements will be noticed, hence such insects show a fright response to an approaching object and shadow.

To postulate thus a basic rate of image displacement which is tolerated by a moving insect is not the same as to say that when an insect is walking all response to image displacement is blocked. This idea has been refuted by von Holst and Mittelstaedt (1950, 1953). It merely means that certain speeds of image displacement lower than the insect's speed do not register as movement.

Possible elaboration of an integrating system dealing with visual stimuli.

A brief word may be added on at least one of the ways in which an integrating system dealing with stimulation of the visual receptors by moving contours could be elaborated. A system which merely notes the total quantity of stimulation is one incapable of fine discrimination. It is to be expected that such a system would be the only one operating in

conjunction with certain visual receptors, e.g. simple intensity receptors, and also with other senses, apart from the visual ones, which werenot highly developed. That this is so is beautifully exemplified by the tactile sense in Octopus, the animal merely responding to the quantity of stimulation and being unable to discriminate between different arrangements (patterns) of equal quantities (Wells and Wells 1957).

The next stage might be that the system could separate the movement of the contour from the pattern of the contour. This pattern would be most simply registered with respect to vetical and horizontal co-ordination on a grid system. The compound eye would, of course, form an excellent grid system, the pattern being registered in terms of vertical and horizontal rows of ommatidia stimulated. Such a system may well exist in the case of the locust nymphs allowing them to discriminate between vertical edges and horizontal, oblique, serrated or wavy edges. Such a system has already been postulated in the case of Octopus (Sutherland 1957a, 1957b).

Finally, it might be conceived that the pattern of stimulation was registered independently of vertical and horizontal co-ordinates and of absolute quantities ~~but~~ and merely in terms of ratios of quantities of stimulation (e.g. see Deutsch 1955). This would enable the animal to recognise a figure at any angle to the vertical and of any size.

It is not suggested that an animal could possess only one of these above systems. On the contrary an animal possessing the system in a highly elaborated form would also possess the lower levels of integration and it is to be expected that it would use these in situations where it

was impossible by virtue of the nature of the stimuli, to use any other. For example, bees merely measure quantity of stimulation when choosing between two flickering lights (Wolf and Zerrahn-Wolf, 1934), but this is apparently not the complete basis of their form discrimination (Hertz 1935).

The above has been limited to the consideration of one type of integration system but others could be postulated. In the case of locusts the system proposed might be susceptible of experimental testing at several points and without this further speculation is unwarranted.

From this discussion it is clear that the system of integration set forth in this thesis is completely compatible with the experimental data obtained. Furthermore the theories mentioned above dealing with the cases of other animals suggest that this system may well be the basic one for the organization of visual information in all animals with well-developed vision.

CONCLUSION.

This work has dealt with a few of the visual responses shown by nymphs of the Desert Locust. Although there is no doubt that these responses form only a fraction of all the responses mediated by vision, nevertheless sufficient information has been obtained to show that the insect has a highly developed visual sense and that its compound eyes are fairly efficient navigating instruments.

The responses which were analysed in detail were form perception, peering, release of antenna movements and various responses to movement. These analyses all point to the importance of one particular type of visual information - displacement of images over the retina. The responses studied are either responses to such stimulation as in the case of attraction to form, antenna movement, optomotor and fright responses, or pieces of behaviour which enable the insect to collect such information viz. peering. It is thus concluded that movement of images over the retina is a highly important stimulus for this insect. While it would be obviously untrue to say that this stimulus lies at the basis of all the insect's "visual" behaviour, it may form the basis of a large part of it. Comparison with results obtained for other insects strongly indicates that the foregoing is true of all insects which use the visual sense to any considerable degree. From such evidence as is presented in this thesis an insight may thus be gained into the "visual world" of the insect.

SUMMARY.

I. The investigation reported here is concerned with the study of certain visual responses in the Desert Locust Schistocerca gregaria, (Forskål). It is a behaviour study. The aim is to form some idea of the kind of information which the insect is obtaining by means of the compound eyes and the way in which this is manipulated.

II. Form perception.

a. In spontaneous choice experiments it is shown that nymphs of the Desert Locust are attracted to black objects on a white background and to the contour lines of these objects. The degree of contrast between the object and the background is important. On a white background the darker the object the more attractive it is.

b. By a series of elimination tests it is shown that straight vertical edges of a figure are attractive features. The longer the vertical edge and the greater the number of vertical edges the more attractive the figure. A straight vertical edge is preferred to a straight oblique edge of the same vertical height. A vertical figure with a straight edge is preferred to a vertical figure with a wavy or a serrated edge.

c. Different figural properties can be balanced against each other. A tall, serrated figure is preferred to a short straight, vertical one.

d. A three inch cross is preferred to a circle of three inches diameter.

e. In the absence of a vertical edge the articulation of a figure is important. Thus both an eight- and a sixteen-pointed star are preferred to a circle.

f. The results of the experiments are compared with those obtained by other workers for other insects and the basis of form discrimination in the Desert Locust is discussed.

III. Peering.

a. It is shown that the swaying of the front part of the body and the head from side to side, called peering, is a visual response. An apparatus is described for measuring the angle through which the head moves laterally with respect to the original position of the longitudinal axis of the body. This is called the peering angle. The angle of peering is affected by the position of objects in the visual field.

b. Peering is also a prelude to a change in direction of locomotion, there being a close correlation between the angle of peering and the subsequent track of the insect.

c. It is also shown that peering is a means of estimating distance, the insect measuring the amount of displacement of object images across the retina as the head moves from side to side. When two objects are so arranged as to appear of the same size although one is twice as distant as the other, the insects

spontaneously choose the nearer object. The choice can, however, be altered by the addition of extra vertical or horizontal contours to the more distant figure. The importance of this and of the peering method of distance estimation is discussed.

IV. Antenna waving.

a. Two main types of antenna movement are distinguished - flicking and beating. The former is a movement of one antenna usually occurring as the insect passes an object. The latter is the alternate movement of both antennae as the insect is approaching head-on and close to an object.

b. Flicking: The antenna to be flicked is the one on the same side as the object and the response occurs when the edge of the object is seen by the more lateral part of the eye. In conjunction with the flicking, the antenna in question is often pointed at the object edge.

c. Beating: This takes place at a short distance from an object (less than one inch), the distance being independent of the angle subtended by the object. The distance at which the response occurs can be altered by altering the position of the base line of the object. The perception of a base line alone is not, however, sufficient to release the response. An essential part of the stimulus situation appears to be the perception of either a horizontal or vertical object in front of the insect. The results suggest that a dark object may have more effect in re-

leasing the response than a light object. It is possible that the stimulus produced by a large object results in a lowering of the threshold so that in some cases the response may be released at a slightly greater distance from the object than in the case of a smaller object.

d. The necessary stimuli for releasing the beating response are discussed.

e. The biological significance of antennae movements as released by visual stimuli is discussed and it is concluded that their main function is to check the information from the visual senses by means of other senses on the antennae.

f. The estimating of an object's distance by the position of the base line may be an example of the use of secondary clues for distance.

V. Responses to movement.

a. Fright response: The insects show a fright response to the movement of a large object across the visual field. The response varies in intensity. At low intensity the insect tenses; at higher intensity the insect jerks; at the highest intensity observed the insect moves (backs or moves sideways) away from the object. The response decreases with increased distance.

b. Optomotor response: The insects show an optomotor response to moving stripes. They follow the movement of the stripes. The stimulus is effective even when it only occupies a small part of

the visual field and the insects respond to stripes moving from front to rear of the eye and from rear to front. Moving stripes stimulating the anterior part of the eye appear to have less effect in releasing the optomotor response than when stimulating the lateral parts of the eye. The insects walk towards a steady movement of stripes in front of them. If the stripe movement is intermittent the insects show the fright response.

c. The Buddenbrock experiment: An experiment is described in which the insects are made to walk down a corridor between two walls decorated with patterns of stripes. When each wall has the same pattern and the insect is equidistant from each wall there is no bias to either side. The insects deviate towards the finer pattern (if equidistant from each) or towards the nearer pattern (if both are equally fine). When presented with vertical and horizontal patterns of equal fineness and at equal distance they deviate towards the former. The importance of speed of image movement and of vertical contours as shown by this experiment is discussed and the results compared with those of previous workers.

d. The differentiation of subject and object movement: Subject movement is the term used to describe the situation in which there is movement of images across the retina arising from the insect's own locomotion in a stationary environment. Object movement refers to the situation in which the insect is stationary and the movement of images across the retina is due to the actual movement of objects

in the environment. An experiment is described to test whether or not the locust nymphs differentiate between the two situations. It appears that they do. Walking insects behave normally in a stationary environment and will walk under an object overhead. Stationary insects show the fright response when the environment moves past them and an object passes overhead. The significance of this is discussed as well as the possible weaknesses of the experiment.

VI. Discussion.

The results of all the experiments are discussed and a system proposed whereby the insect responds to the stimulation of the visual receptors produced by the movement of the images of contours over the retina. The properties of the system are discussed as well as the behaviour which would be expected as the results of these. A comparison is then made with the behaviour observed in the present investigation. One possible way in which such a system could be elaborated is briefly considered.

VII. Conclusion.

The conclusions is reached that, although the work has dealt with only few of the visual responses of these insects, sufficient information has been obtained to show that the insects possess a highly developed visual sense, that their compound eyes are quite efficient navigating instruments and that visual responses play a large part in the total behaviour repertoire. The analyses of the stimuli involved in each response studied gives some insight into the nature of this insect's visual environment.

APPENDIX.

The vision of the apposition eye.

Underlying most previous work on insect vision has been the mosaic theory of image formation by the apposition eye (Müller 1829 in Wigglesworth 1953). This theory supposes that each ommatidium in the eye receives light from only a very limited region of the visual field. Thus, "each ommatidium receives the impression of a luminous area corresponding to its projection on the visual field". (Wigglesworth 1953).

Recently, however, it has been shown that the theory is at variance with the facts. Burtt and Catton (1954) showed that in Locusta migratoria migratorioides and in the hive bee the visual fields of the ommatidia overlap to a considerable extent and are not discrete. Waterman has also demonstrated this in the eye of Limulus (Waterman ~~1953~~, 1954).

In this appendix it is desired to draw attention to the fact that such overlap of receptive fields of single sensory fibres is a common property of many sensory receptors, e.g. the vertebrate skin and retina (Granit 1955). It is important to note that in the cases quoted and par excellence in the retina very fine discrimination is possible, i.e. overlap does not preclude fine discrimination. The various ways in which this may be achieved are discussed by Granit in his book (1955).(loc.cit.)

The good correlation obtained in some work (Gavel 1940; Hassenstein 1951) between ommatidial angle and the effects of stimuli at certain definite distances apart suggests that there is an underlying neural mech-

anism which allows the ommatidium to act as a functional unit. In cases where there is no correlation between these quantities (e.g. Bröcker 1935) this may be due to the neural mechanism involved.

Theories based on the unitary action of the ommatidium are not necessarily invalidated by the discovery of overlap.

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TABLES

Table 38.

Table showing summary of responses of locust nymphs to different conditions of movement of the environment. (a) insect stationary environment moving. (b) insect walking environment stationary. (c) control insect and environment moved together (see text).

	Conditions	No. of Animals	No. of Fright Resp.		No. of other Resp.			
			Possible	Actual.	Motion-less	Climb-ing on Wall	Waving Ant-ennae	Walk-ing
a	Apparatus Moving, Animal Stationary	31	62	37	11	2	1	11
b	Apparatus Stationary Animal Moving.	28	52	0	46 walked on 6 stopped			
c	Control	10	20	0	8			10
					2 walked then stopped.			

The significance of the number of fright resonses in each condition is obvious without statistical analysis.

Table 37.

Table showing bias in locust nymphs walking carried by a response to striped patterns. (von Buddenbrock expt. Figs. 22, 23).

	Conditions		Bias				
	Stripes	Position of Runway	Right	Left	Centre	Sig. X^2	Animals
1	1" wide 8" tall on each side.	4.5 from either wall.	80	73	97	.2 > P > .1	6
	"	3"R 6"L	72	22	9	P < .01	3
	"	3"L 6"R	27	104	33	P < .01	4
2	1" wide 8" tall R. 1" wide, 4" tall L.	Control 4.5" L.R.	25	5	127	P < .01	5
	"	Expt. 3L. 6R	33	86	144	P < .01	6
3	1" Vertical/4.5" R. 1" Horizontal L.	from either wall.	Vert. 104	Hor. 5	C 79	P < .01	5
4	1" stripes 4.5" R. & L. R. 2" stripes L.		90	38	155	P < .01	5
	1" stripes L 4.5 R. & L. 2" stripes R.		44	95	77	P < .01	5

By X^2 test degrees of freedom = 2.

Table 36.

Table showing the number of responses of different types obtained when the insects are facing moving stripes. The movement is confined to a sector of 30° of the visual field. Uniform stimulation - produced by continuous movement of alternating 1" black and white stripes at varying speeds. Intermittent stimulation - produced by two black stripes 4" broad diametrically opposite on white cylinder of 54" circumference.

Stimulus	No. of Animals	Response		
		Attraction	Fright	No Response
27 changes/ sec.Uniform	4	16	0	4
Uniform 11 hanges/sec.	4	11	0	9
Intermittent 2 changes/ sec.	9	1	30	14
Stationary (Control)	4	16	1	3

The above results are sufficiently obvious without statistical analysis.

Response to Movement (Tables 35 - 38).

Table 35.

Table showing number of fright responses to a moving object at different distances from the object.

	Position and Distance of Object.					
	9" front	9" side	18" front	18" side	24" front	36" front
No. of Res-	7.9	3.0	4.6	-	-	-
ponses out	6.7	2.8	4.2	0	-	-
of 10 poss-	7.8	3.1	3.9	-	-	-
ibles (Each	-	-	-	-	2.5	-
is the aver-	7.1	-	-	-	-	1.0
age for 10	-	-	-	-	-	.6
animals.						
Final Aver.	7.37	2.9	4.2	0	2.5	.8

- = no test performed. 0 = no response obtained. Figures in horizontal rows were obtained for the same 10 animals in the different situations. Figures in different rows refer to different groups of 10.

Table 33.

Table showing number of cases where antenna beating (or dipping) was observed as locust nymphs walked across the boundary between 2 equally large flat areas 1 black one white. Readings were taken for both directions of walking. + = response observed. - no response.

	Direction of Walking			
	White - Black		Black - White	
Animal	+	-	+	-
1	5	0	5	0
2	5	0	4	1
3	4	1	4	1
4	5	0	2	3
5	5	0	1	4
6	5	0	4	1
7	5	0	5	0
8	5	0	3	2
Total	39	1	28	12
	n = 40			

39:1 ($P < .01$) 28:12 ($P < .01$)

Comparing 39:1) $P < .01$
28:12)

Table 34.

Table showing number of cases in which antenna beating was observed as a locust nymph walking on a plain white floor approached a large vertical plain black wall. + = response observed. - = no response.

Animal	+	-
1	5	0
2	3	2
3	2	3
4	5	0
5	4	1
6	5	0
7	3	2
8	5	0
9	2	3
	34	11

34:11 $P < .01$.

Table 32.

Table showing number of cases where antenna beating was observed as locust nymphs walked along a narrow run ay, half of which was white and half black. Responses occurred at the joining of the black and white regions. The insects were observed when walking from white → black and also in the opposite direction. + = response observed. - no response.

	Direction of Walking			
	White → Black		Black → White	
Animals	+	-	+	-
1	5	0	0	5
2	5	0	1	4
3	4	1	1	4
4	5	0	1	4
5	2	3	0	5
6	5	0	2	3
7	5	0	1	4
8	2	3	0	5
9	3	2	2	3
10	4	1	0	5
Total	40	10	8	42

40:10 $P < .01$ 8:42 $P < .01$

Comparing 40:10) $P < .01$
8:42)

Table 31.

Table showing number of cases where antenna beating was observed in the 2 conditions mentioned. + = response observed - no response.

Animal	Plain White Object (Control)		White Object, Black Edges	
	+	-	+	-
1	1	4	4	1
2	2	3	4	1
3	0	5	3	2
4	0	5	3	2
5	2	3	5	0
6	2	3	3	2
7	0	5	5	0
8	4	1	5	0
9	0	5	3	2
10	3	2	5	0
Total	14	36	40	10

40:10

14:36 $P < .01$ $P < .01$ (by the X^2 test)

Comparing 14:36) $P < .01$ by the X^2 test.
40:10)

Table 30.

Table showing number of cases where antenna beating was observed for different conditions of floor and object. + = response observed - = no response.

Animal	Experiment White Object, Black Floor.		Control Black Object White Floor		Control White Object White Floor	
	+	-	+	-	+	-
1	2	3	5	0	2	3
2	0	5	-	-	2	3
3	0	5	4	1	0	5
4	0	5	5	0	0	5
5	3	2	4	1	2	3
Total	5	20	18	2	6	19

5:20, 18:2, 6:19 $P < .01$ in each case by the X^2 test.

Comparing 5:20) No significant difference.
6:19)

Comparing 5:20) $P < .01$
18:2)

Table 29.

Table showing distances in inches at which antenna beating commenced as locust nymphs approached a black object with a false base line painted on the floor 3" from the real base of the object. Note in most cases the insects beat their antennae on reaching the false base line. + = antenna beating observed. - = no response.

Animal	Distance in inches at which beating occurred.					+	-	Average distance of +
	1	2	3	4	5			
1	3.5	3	3	3.25	2.5	2	3	3.37
2	3	2.5	2.5	3	3	0	5	-
3	3.5	3.5	3.25	3.5	3.5	5	0	3.45
4	3.5	3.5	3.75	3.5	3.5	5	0	3.57
5	3.25	3.25	3.25	3.5	3.25	5	0	3.3
6	3.5	3.5	3.25	3.25	3.0	4	1	3.37
7	3.0	3.25	1.5	3.0	.5	1	4	3.25
8	1.0	3.5	3.0	3.25	3.25	3	2	3.33
9	3.5	3.5	3.5	3.75	3.5	5.	0	3.55
10	3.5	3.25	2.5	3.0	3.0	2	3	3.37
11	3.25	3.25	3.0	3.5	3.5	4	1	3.32
12	3.5	4.0	3.5	3.25	3.25	5	0	3.5
13	3.5	3.5	3.5	3.25	3.25	5	0	3.4
14	3.75	3.5	3.5	3.5	3.25	5	0	3.5
15	3.25	3.25	3.25	3.5	3.5	5	0	3.35
16	3.5	3.5	3.5	3.25	3.25	5	0	3.4
17	3.5	3.5	3.5	3.25	3.5	5	0	3.45
18	3.5	3.25	3.5	3.5	3.0	4	1	3.3
19	3.25	3.0	.25	3.0	.25	1	4	3.25
20	3.25	3.0	3.0	3.25	3.25	3	2	3.25
				Total		74	26	Aver. 3.38
								= 3.4"

Comparing 74:26 $P < .01$.

Table 28.

Table showing the number of cases in which antenna beating was seen (1) when the object was raised off the runway (expt. 4) (2) when the object was sitting on the runway (control). (See Fig.18 Expt.5).
+ = antenna beating observed. - = no response.

	Experiment		Control	
Animal	Object off floor			
	+	-	+	-
1	2	3	5	0
2	2	3	5	0
3	1	4	4	1
4	3	2	5	0
5	1	4	4	1
6	3	2	5	0
7	0	5	5	0
8	3	2	5	0
9	0	5	5	0
10	1	4	5	0
11	1	4	5	0
12	1	4	4	1
13	0	5	5	0
14	1	4	3	2
15	1	4	5	0
16	1	4	Total 70	5
17	5	0	n = 75	
18	5	0		
19	0	5		
20	2	3		
21	4	1		
22	1	4		
n = 110	38	72		

Comparing 38:72 $P < .01$

70: 5 $P < .01$

38:72)
70: 5) $P < .01$

results tested by the X^2 test in each case.

Table 27.

Table showing distances in inches at which atenna beating commenced as locust nymphs approached black objects of different sizes. A comparison of the means .65, .76 and .82 showed that they did not differ significantly from one another. Comparing .76:.82 ($P > .5$) Comparing .65:.82 ($.1 > P > .05$). Comparison of the variance in each case showed that there was a significant difference between them. Comparing 0.0728: 0.34754 ($P < .01$). Comparing 0.0728 : 0.1331 ($P < .05$) Comparing .1331 : 0.3754 ($P < .01$).

Object	Distances in inches at which beating commenced for each size of object.																	
	4" tall X 1" broad						12" tall X 1" breed						4" tall X 12" broad					
	Runs						Runs						Runs					
Animal	1	2	3	4	5	Av.	Animal	1	2	3	4	5	Av.	Animal	1	2	3	4	5	Av
1	.5	.75	.75	.5	.5	.6	1	.5	.5	.5	.5	.5	.5	1	.75	.5	1.0	.5	1.0	.75
2	1.0	.75	1.25	.5	1.0	.9	2	.5	.25	.5	1.0	.5	.55	2	1.0	1.0	.25	.5	.75	.7
3	.5	.75	.25	.5	.75	.55	3	1.0	.5	.5	.5	.25	.55	3	1.0	1.0	3.0	3.0	3.0	1.9
4	.25	.5	.5	.5	.5	.45	4	.75	1.0	.5	.75	.5	.7	4	.75	2.0	.5	.5	.5	.85
5	.5	.75	.5	.5	.5	.55	5	1.0	1.0	.75	2.0	2.0	1.9	5	1.5	.5	.5	.5	1.0	.8
6	1.25	1.5	1.0	.75	1.0	1.1	6	.75	.75	1.0	1.25	-	.75	6	.5	.5	1.0	.25	.75	.6
7	.5	.5	.5	.75	.5	.55	7	1.0	1.0	1.0	1.0	1.0	1.0	7	.25	.5	.5.	.5	.5	.45
8	1.0	1.0	.5	.75	.75	.8	8	.75	.5	.5	.5	.5	.55	8	.75	1.0	1.0	.5	.5	.75
9	.25	.5	1.0	.5	.5	.55	9	.5	.25	.5	.5	.75	.5	9	1.5	.25	.5	.5	.25	.6
10	.5	.5	.5	.5	.5	.5	10	.5	1.25	.75	.5	.5	.7	10	.75	.25	1.5	.75	1.0	.85
n = 50	Final Average					.65	n = 50	Final Average					.76	n = 50	Final Average					.82
	Variance .0728							Variance .1331							Variance .34754					

Table 26.

Table showing the relation between the position of one edge of an object which is approached obliquely and the position of the first antenna flick. The relationship is expressed as the bearing in degrees of the former from the latter.

Approach Angle	Animal	Object 4" tall X 6" broad. Bearing of C in o's from position of 1st flick. Runs 1	2	3	4	5	Average
30	1	40	80	50	40	40	50
"	2	40	70	80	90	60	68
"	3	60	60	-ve	70	80	67.5
"	4	60	30	80	70	80	64
"	5	70	40	70	70	80	66
		Final Average					63
60	1	40	90	60	60	50	60
"	2	70	60	70	70	60	66
"	3	40	70	40	60	70	56
"	4	70	70	40	80	40	60
"	5	70	70	70	70	70	70
		Final Average					62
		Object 4" tall X 1" broad					
Approach	Animal	Bearing of C in o's from position of 1st flick					Average
30	1	50	40	70	40	80	56
	2	60	60	60	80	90	70
	3	50	50	70	60	60	58
	4	30	40	60	50	60	48
	5	50	40	60	60	40	50
		Final Average					56.4

Antenna Waving (Tables 25 - 34)

Table 25.

Table showing the direction of an insect's approach to an object in relation to the first antenna flick. Approach - for meaning of the terms see Fig.14. + indicates that the first antenna to be flicked was the one nearest to the object. - indicates that the first antenna to be flicked was not the one nearest the object.

Approach	1st Antenna flicked	+ or -	Distance in inches
Front	Left	-	5
Front	Both	+	1.5
Front	Both	+	2.0
Front	Both	+	2.0
Left	Left	+	3.5
Right	Right	+	4.0
Left	Left	+	3.0
Front	Both	+	4.0
Right	Left	-	5.0
Left	Left	+	2.5
Front	Both	+	1.5
Left	Left	+	2.5
Left	Left	+	4.0
Right	Right	+	3.5
Right	Both	-	4.0
Right	Right	+	3.0
Right	Both	-	3.0
Right	Right	+	4.0
Right	Right	+	5.0
Right	Right	+	5.0
Left	Left	+	5.0
Front	Both	+	1.5
Front	Both	+	1.0
Front	Both	+	5.0
Left	Left	+	4.0
Right	Left	-	5.0
Right	Right	+	3.0
Right	Right	+	5.0
Front	Both	+	2.0
Front	Left	-	4.0
Left	Left	+	5.0
Left	Left	+	2.0
Right	Right	+	5.0
Total 33		+ 27 - 6	

Comparing 27 : 6, $P < .01$.

Table 24.

Results of jumping experiment with single moving object. (See text).

S = jumped short. O = overshot.

	Stationary Object				Object Moving Against Insect				
Animal	Hit	Miss	S	O	Hit		Miss	S	O
1	4	1	-	-	0		5	5	-
2	8	1	-	1	1		5	5	-
3	5	0	-	-	0		5	5	-
4	5	0	-	-	0		5	5	-
5	5	0	-	-	0		5	5	-
6	4	2	2	2	0		3	3	-
7	3	2	2	-	0	(2)	3	3	-
8	8	0	-	-	0		7	7	-
	42	6	4	1	1		38	38	0

	Object Stationary				Object moving with Insect				Object moving against insect			
Animal	Hit	Miss	S	O	Hit	Miss	S	O	Hit	Miss	S	O
1	5	0	-	-	5	0	-	-	0	3	3	-
2	5	1	-	1	3	2	-	2	0	3	3	-
3	3	0	-	-	3	2	1	1	0	2	2	-
4	6	1	-	1	3	3	2	1	0	2	2	-
	19	2	-	2	14	7	3	4	0	10	10	-

S = jumped short

O = overshot

Table 23.

Summary of conditions and results of tests 8a - 8d (Expt. 3).

Numbers in brackets represent number of jumpt not aimed at either object.

Test	Experimental Conditions		Choice	Total
	Near Object	Distant Object	N D	
8a	Plain Black 6" X 1 at 3" 45oL	Vertically striped Black/White 12 X 2 at 6" 45°R	8 17 9(1)15	25
8b	Plain Black 6 X 1 at 3" 45°L	Hor.striped Black/ White 12 X 2 at 6" 45°R	9(1)15	25
8c	Horizontally Striped Object	Vertically striped Object	H V	
	Left	Right	6 19	25
	Right	Left	6 19	25
8d Control	Plain Black 6 X 1 at 3" 45°L	Plain Black 12 X 2 at 6" 45°R	24(1) 0	25

Tables 21-23. Note. While it would have been better perhaps to randomise the presentation for each animal with regard to side, nevertheless comparison of tests 1 & 2, and 6 & 7 (table 21) and tests 8a & 8d and 8b & 8d (table 23) and consideration of 8c obviates the possibility of all position effect.

Comparing Control 24 : 0 }
Expt.8a 17 : 32 }..... p .01 (by X^2)
Expt.8c 12 : 38..... p .01 (by X^2)

Comparing: Control v 24 : 0 }
Expt.8b 9 : 15 }..... p .01 (by X^2)

Table 22b.

Further summarising of results of Table 22a showing correlation between directions of second orientation and final choice of object.

Test	No. of Initial Orientations at 0°.	No. of cases where 2nd Orientation coincided with final choice.	No. of cases where 2nd Orientation did not coincide.
1	13	11	2
2	14	14	0
4c	15	15	0
5	13	8 (1)	4
8a	26	20	6

Table 22a.

Table showing the frequency and order of orientations made prior to jumping on one of 2 objects. (Tests 1, 2, 4a, 5, 8a, see text).

Orientations. O = along line of 0°

N = to one side of the 0° line. The side of the nearer object.

D = to one side of the 0° line. The side of the more distant object.

Choice N or D indicates final jump on near or distant object respectively.

1 - 5 indicates temporal sequence of orientations.

	Order of Orientations										Final Choice		
	1			2			3			4			5					
Test	O	N	D	O	N	D	O	N	D	O	N	D	O	N	D	O	N	D
1	13	7	5	1	19	5	-	9	-	-	3	-	-	-	-	-	23	2
		25			25			9			3			0				
2	14	7	4	-	18	2	-	7	-	-	-	-	-	-	-	-	23	2
		25			20			7			0			0				
4c	15	7	2	1	18	4	-	10	-	-	3	-	-	-	-	3	20	2
		24			23			10			3							
	Animals blinded in anterior quarter of Near eye																	
5	13	2	5	1	12	5	-	9	2	-	2	1	-	-	-	1	14	5
		20			18			11			3							
8a	26	6	17	-	14	23	-	3	9	-	2	-	-	-	-	1	17	32
		49			37			12			2							

Table 22.

Table showing body orientation while insect peered in a situation with 2 objects lying 45° to the left and right. (For further description see text p.55-58). The orientations were measured with respect to a 0° line mid-way between both objects. Orientations marked N and D represent orientation to the side of the nearer and more distant object respectively. N and D in the jumping column indicate the object to which the insect finally jumped.

Animal	Body Orientation to nearest 5°				Jump N	Jump D
1	0°	5°D	90°+N	45°N	+	-
	0°	60°N			+	-
	0°	60°N	45°N		+	-
	5°N	10°D	45°N		+	-
	45°N	30°D	20°N	45°N	+	-
2	0°	20°N			+	-
	0°	10°N	30°N		+	-
	0°	45°N			+	-
	5°D	20°N	30°N		+	-
	0°	30°N			+	-
3	0°	45°N			+	-
	10°D	0°	20°N		+	-
	5°N	25°N		+	+	-
	0°	10°D			-	+
	10°N	20°N			+	-
4	0°	45°N			+	-
	10°D	90°N	20°N	45°N	+	-
	0°	45°N			+	-
	0°	45°N			+	-
	10°N	45°N			+	-
5	10°D	90°N	45°N		+	-
	0°	45°N			+	-
	5°N	45°N			+	-
	10°D	40°D			-	+
	5°N	45°N			+	
				Total	23	2

Table 21.

Table summarising conditions and results of jumping tests 1 - 7 (expt.3) with 2 stationary objects. The columns N & D show the number of jumps made on to the near and distant object respectively. Numbers in brackets represent number of jumps which were not aimed at either object.

	Experimental Conditions		Choice		
Test	Near Object	Distant Object	N	D	TOTAL
1	Black 6 X 1 at 3" 45°L	Black 12 X 2 at 6" 45°R	23	2	25
2	Black 4 X 1 at 3" 45°R	Black 12 X 2 at 6" 45°L	23	2	25
3	a) Grey 6 X 1 at 3" 45°	Black 12 X 2 at 6" 45°	23	2	25
	b) White 6 X 1 at 3" 45°	Black 12 X 2, at 6" 45°	22	3	25
		in each case $p<.01$			
	Partially Blinded Animals				
4	a) Black 6 X 1 at 3" 45°L	Black 12 X 2 at 6" 45°R	9	6	15
			(.5>p>.3)		
	Animals tested after 3 hrs.				
	b) Black 6 X 1 at 3" 45°L	Blakc 12 X 2 at 6" 45°R	14	1	15
			(p<.01)		
	c) "	"	20(3)	2	25
	Partially Blinded animals				
5	Black 4 X 1 at 3" 45°L	Black 8 X 2 at 6" 45°R	14(1)	5	20
			(.05>p>.02)		
	One-eyed Animals				
6	Black 4 X 1 at 3" 80°R	Black 12 X 2 at 6" 30°R	12(1)	2	15
	Completely blinded in left eye.		(p<.01)		
	Partially Blinded Animals				
7	a) Black 4 X 1 at 3" 80°R	Black 12 X 2 at 6" 30°R	15	5	20
			(p<.01)		
	b) Black 4 X 1 at 3"	Black 12 X 2 at 6" 80°R	19	1	20
	¾ of left eye blind.		(p<.01)		

Table 20.

Table showing frequency of occurrence of different sizes of peering angle in a situation where there are objects all round the insect. As in Table 18, the corrected values for a population of 173 are given in the last line.

	Categories of peering angle in degrees.										Runs
	1 - 3		4 - 6		7 - 9		10 - 12		12+		
	L	R	L	R	L	R	L	R	L	R	
Frequency	3	6	9	7	22	4	3	0	0	1	22
	5	4	7	6	4	10	1	1	-	-	17
	7	6	15	11	5	7	5	11	2	0	21
Total L R	15	16	31	24	31	21	9	12	2	1	60
Total	31		55		52		21		3		
	Total population n = 162										
	Corrected values n = 173										
Total	33.1		58.7		55.5		22.4		3.2		

Table 19.

Table showing details of peering angles recorded and the angle of the insect's subsequent track (see Fig. 8.) "Order 1,2" etc., represents first peering angle, second peering angle, etc. A correlation coefficient was calculated to test the correlation between the verage peering angle and the angle of the subsequent track. The correlation is significant. $r = 0.455$.

	Peering Angles in ° Order				Av. Peer. Ang. in°	Ang. Sub. Trk. in °		Peering Angles in ° Order				Av. Peer. Ang. in°	Ang. Sub. Trk. in °
	1	2	3	4				1	2	3	4		
1	11R	9R	-	-	10R	55R	21	6L	10L	9L	-	8.3L	40L
2	4R	-	-		4R	16R	22	5R	10R	-	-	7.5R	15R
3	10R	9R	4L	8R 9R	9R	65R	23	9R	8R	8R	-	8.3R	35R
4	7L	-	-	-	7L	20L	24	4R	4R	-	-	4R	10R
5	4R	7L	-	-	7L	50L	25	7R	7R	-	-	7R	15R
6	5L	-	-	-	5L	30L	26	5R	5R	-	-	5R	15R
7	6L	-	-	-	6L	25L	27	6L	6L	-	-	6L	35L
8	5L	1R	-	-	5L	10L	28	4R	10R	-	-	7R	90R
9	6R	-	-	-	6R	12R	29	3R	3L	5R	-	4R	50R
10	7L	7L	-	-	7L	30L	30	7L	7L	-	-	7L	25L
11	10L	9L	7L	8L	8.5L	90L	31	5L	12L	-	-	8.5L	75L
12	18L	10L	-	-	10L	20L	32	10R	10R	-	-	10R	90R
13	7L	-	-	-	7L	35L	33	9R	6R	-	-	7.5R	40R
14	8L	8L	-	-	8L	50L	34	11R	-	-	-	11R	30R
15	6R	-	-	-	6R	35R	35	1L	6R	-	-	6R	20R
16	15R	-	-	-	15R	30R	36	11L	8L	-	-	9.5L	50L
17	6R	6R	-	-	6R	10R	37	11L	3R	9L	10L	10L	45L
18	8R	-	-	-	8R	20R	38	10R	-	-	-	10R	55R
19	5L	5L	-	-	5L	5L	39	13L	13L	-	-	13L	55L
20	6L	-	-	-	6L	25L	40	4L	-	-	-	4L	25L

Table 18.

Table showing frequency of certain sizes of peering angle when there is a single object 40° - 60° to the right of the insect. (See Fig. 4b).

	Categories in °s.								
	1 - 3		4 - 6		7 - 9		10 - 12		Runs
Left or Right	L	R	L	R	L	R	L	R	
	10	3	12	6	8	9	4	7	22
Frequency	6	6	4	10	4	10	2	2	31
	10	5	11	12	7	16	0	9	24
Total L & R	26	14	27	28	19	35	6	18	77
Total	40		55		54		24		
	Total population = 173								

Peering.(Tables 17 - 24).

Table 17.

Table showing frequency of occurrence of certain sizes of peering angle when there is an object subtending 20° in front of the insect (see Fig. 4a). The sizes of angle are divided into 4 categories. L = frequency of occurrence of "left" peering angles; R = frequency of occurrence of "right" perring angles. Corrected values - the values for a population of 173 results are given in the last 2 lines so as to allow comparison with those of tables 18 and 20.

	Categories in °s.								
	1 - 3		4 - 6		7 - 9		10 - 12		Runs
Left or Right	L	R	L	R	L	R	L	R	
	5	5	8	8	8	5	3	2	15
Frequency	15	15	23	18	0	4	0	4	21
Total L & R	20	20	31	26	8	9	3	6	
Total in each group	40		57		17		9		36
			Total population = 123.						
	Corrected Values								
Total L & R.	28	28	43.4	36.4	11.2	12.6	4.2	8.4	
Total in each group	56		79.8		23.8		12.6		
	Total population = 173								

Note: In the above table and in the case of the results in tables 18 and 20 which are similar, the significance of the distribution of ppering angles to right and left is arrived at by comparing the frequencies in each case by X^2 test.

Table 15.

Animals	Cross	Circle	Others	P
10	27	12	11	.02 > P > .01
10	26	9	15	< .01
Total 20 n = 100	53	21	26	< .01

Table 16a.

Animals	16 Point Star.	Circle	Others	P
10	27	14	9	.05 > P > .02
10	32	13	5	< .01
Total 20 n = 100	59	27	14	< .01

Table 16b.

Animals	8 Point Star.	Circle	Others	P
5	11	5	9	.3 > p > .1
7	19	7	9	.02 > p > .01
Total 12 n = 60	30	12	18	< .01

Table 13a.

Narrow Serrated.

Animals	Straight	Serrated	Others	P
10	26	16	8	.2 > P > .1
10	30	17	3	.05 > P > .02
10	24	20	6	.3 > P > .2
10	34	12	4	< .01
40 n = 200	114	65	21	< .01

Total

Table 13b.

Broad Serrated.

Animals	Straight	Serrated	Others	P
11 n = 55	30	15	10	.05 > P > .02

Table 14a.

Animals	Tall Serrated	Short Straight	Others	P
5	15	5	5	<.01
5	17	5	3	<.01
5	12	3	10	<.01
15 n = 75	44	13	18	P<.01

Total

Table 14b.

Animals	Tall Serrated	Tall Straight	Others	P
15 n = 75	24	46	5	< .01

Table 9.

Animals	Erect	Horizontal	Others	P
8 n = 40	17	9	14	.2 > P > .1
10 n = 50	26	8	16	< .01
Total 18 n = 90	43	17	30	< .01

Table 10.

Animals	High	Low	Others	P
10	12	27	11	.02 > P > .01

Table 11.

Animals	Straight vert. edge	Straight obliq.edge	Others	P
7 n = 35	20	13	2	.3>p>.2
5 n = 25	20	4	1	<.01
Total n = 60	40	17	3	< .01

Table 12.

Animals	Straight	Wavy	Others	P
10 n = 50	39	8	3	< .01
10 n = 50	36	12	2	< .01
Total 20 n = 100	75	20	5	< .01
	4th Instar			
15 n = 75	46	18	11	< .01

Table 5a.

Animals	Broad	Narrow	Others	P
10 n = 100	22	66	12	$P < .01$

Table 5b.

Animals	Broad	Narrow	Others	P
10 n = 50	9	28	13	$P < .01$

Table 6.

	Animals	Broad	Narrow	Others	P
Expt.	20 n = 100	41	30	29	$.2 > P > .1$
Control	10 n = 50	16	26	8	$P < .01$ Comparing Expt. & Control.

Table 7.

Animals	Broad	Narrow	Others	P
10 n = 50	23	16	11	$P \geq .2$
10 n = 50	27	13	10	$.05 > p > .02$
Total 20 n = 100	50	29	21	$.02 > P \geq .01$

Table 8.

	Animals	Tall	Short	Others	P
Expt.	10	37	6	7	$< .01$
	10	35	3	12	$< .01$
Total	20 n = 100	72	9	19	$< .01$
Control	10	No tall stripes	32	13	$< .01$

Table 3.

Animals	Black	Grey I	Others	P
	-	4	1	
	2	3	0	
	1	1	3	
	5	0	0	
	4	1	0	
	4	1	0	
	1	3	1	
	2	2	1	
	1	1	3	
	3	1	0	
Total 10	23	17	10	.5 > P > .3

Table 4a.

Animals	Black	Grey II	Others	P
5th Schistocerca 11 n = 55	31	15	9	.02 > P > .01
4th Schistocerca 20 n = 100	62	28	10	P < .01

Table 4b.

Animals	Grey	White	P
4th Instar 10 n = 50	31	19	

Note the white occupied more than 3 timesthe length of the perimeter occupied by the grey, therefore animals had 3 X more chance of visiting the white.

TABLES.

Form Perception (Tables 1 - 16).

These tables show the number of animals used in each experiment and the number of visits paid to each type of object. "Others" indicate visits to the white wall of the arena (misses).

In the case of tables 2 - 16 "others" (which are misses) are ignored and the number of visits to each type of object compared by X^2.

Table 1.

No. of Animals	No. attracted to Black area	No. attracted to White area	No. attracted to edge	P
30	4	4	22	$< .01$

Table 2.

	No. of Animals	Tall	Short	Others	Edges	P
	10	10			10	
	10	9	1		8	
	10	7	3		9	
	10	8	2		8	
Total	40	34	6		35	$< .01$

Tables.

Note on statistics used.

The X^2 test was used in the following cases:-

Tables 1 - 16, 17, 18, 20, 21, 23, 25, 28-34.

For table 19 the correlation coefficient was calculated from the formula

$$r = \frac{\Sigma(\text{Dev. A. X Dev. B.})}{\sqrt{\Sigma(\text{Dev. } A^2 \; X \; \Sigma \text{Dev.} B^2)}}$$

where A and b are the 2 classes of results to be correlated, in this case av. peering angle and angle of subsequent track.

The results in table 27 were analysed using the "t" test for comparing means. The formula is:-

$$t = \frac{M_1 - M_2}{\sqrt{\left(\frac{\Sigma d_1^2 + \Sigma d_2^2}{n_1 + n_2 - 2}\right)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where M_1 and M_2 are the two arithmetic to be compared.
d_1 and d_2 are the respective deviations
n_1 and n_2 are the two populations.

also in table 27 The variances were compared as follows:-

$$\text{Variance ratio } F = \frac{\text{Variance 1}}{\text{Variance 2}}$$

where variance for each sample = $\frac{d^2}{n - 1}$